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May 1988

Benthic Productivity and Marine Resources of the Gulf of Maine

Ivar Babb and Michael De Luca,
Editors

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Benthic Productivity and Marine Resources of the Gulf of Maine

Ivar Babb and Michael De Luca,
Editors

May 1988



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PREFACE

The Office of Undersea Research of the National Oceanic and Atmospheric Administration (NOAA) supports in situ research utilizing a variety of systems including manned submersibles, saturation habitats, remotely operated vehicles (ROVs), and air and mixed gas scuba. There are currently five National Undersea Research Centers (NURCs) that operate on grants from NOAA. These centers are located at the Caribbean Marine Research Center, Riviera Beach, Florida, the University of Connecticut at Avery Point, Fairleigh Dickinson University at St. Croix, USVI, the University of Hawaii at Manoa, and the University of North Carolina at Wilmington.

NOAA's Office of Undersea Research provides facilities for scientists to conduct research supporting NOAA's mission objectives in the areas of: global oceanic processes, pathways and fate of materials in the ocean and Great Lakes, coastal oceanic and estuarine processes, ocean lithosphere and mineral resources, biological productivity and living resources, diving safety and physiology, and ocean technology.

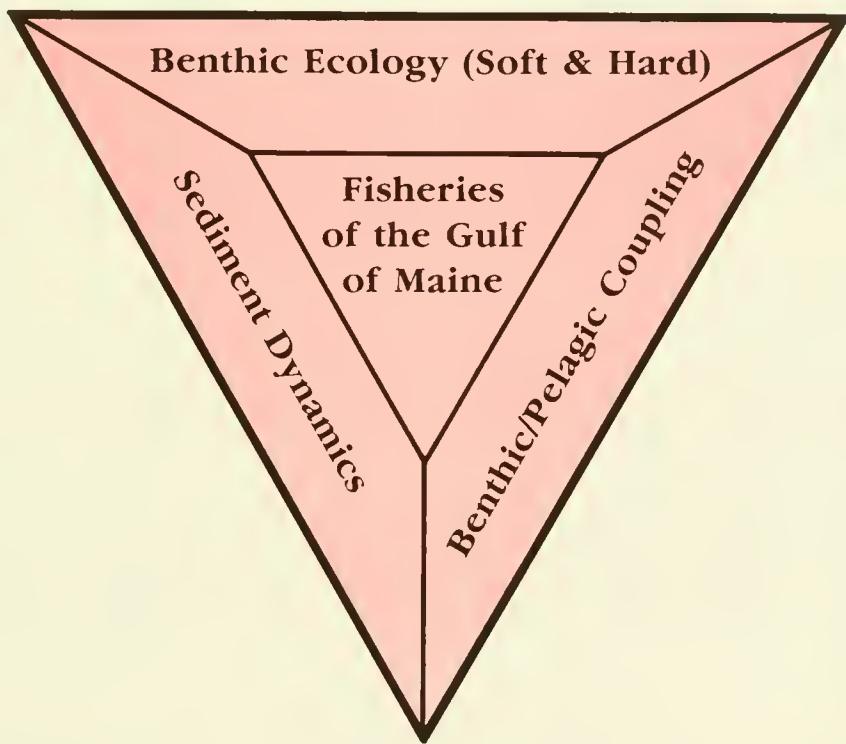
The series of papers presented in this and a companion volume are the result of a symposium held at the National Undersea Research Center, University of Connecticut at Avery Point on October 21-23, 1987. The symposium addressed four major research themes: marine resources in the Gulf of Maine, global vent processes, deep-water ecology, ocean technology, and biological productivity. Papers presented at the symposium are published in two volumes: 1) Benthic Productivity and Marine Resources of the Gulf of Maine and 2) Global Venting, Midwater, and Benthic Ecological Processes. As editors, we undertook to standardize elements of the papers, clarify statements, and in other ways assist the session chairman in the work they performed in assembling these papers. The papers presented herein meet requirements of grantees to the Office of Undersea Research.

We acknowledge Marcia Collie with special thanks for her assistance with the final preparation of these volumes. Her talent for and experience with preparation of the manuscripts to camera-ready copy are sincerely appreciated.

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Benthic Productivity and Marine Resources of the Gulf of Maine



GULF OF MAINE -

OVERVIEW OF RESEARCH STATUS

R. S. Steneck and R. Langton

The Gulf of Maine is famous for its rich fishing grounds, that have remained productive for nearly 400 years yielding groundfishes, shellfish and lobsters. Today, catches in the Gulf of Maine (and Georges Bank) comprise more than 80% of the total landings (in value) for the New England states and of that more than 90% are fishes and invertebrates associated with the sea floor. Despite the history of commercially important bottom dwelling organisms in the Gulf of Maine, limited data exist on their distribution and abundance or how they interact, behave and feed on the sea floor. In fact, our knowledge of the sea floor itself is poor despite its importance to benthic communities as a source of food, habitat and for nutrient regeneration. It is for these reasons that the National Undersea Research Program (NURP) has supported researchers from state and private universities, federal, state and private laboratories for the past four years in a multidisciplinary effort to address the benthic productivity and resources of the Gulf of Maine.

The Gulf of Maine is an oceanographically discrete body of water bounded by land from Cape Cod to Nova Scotia and to the seaward by Georges and Browns Banks. In the recent geologic past the Gulf was scoured by glaciers which created a complex diversity of habitats and environments. To study these components we have identified five habitat-regions within the Gulf. They are: 1) coastal regions comprising the turbid nearshore water, 2) the central gulf, including the smaller banks and ledges, 3) the slope water complex which contains basins and the Northeast Channel, 4) the seaward border, which includes the larger banks (Georges and Browns) and 5) the water column that overlies the entire region and connects it to the western North Atlantic Ocean.

In addition to its topographical complexity the study of the productivity of the Gulf of Maine involves aspects of biological, geological, chemical and physical oceanography. Sampling techniques for bottom dwelling animals and sediments have traditionally involved trawls, drags and grabs which are time-consuming and often give limited or dubious results. Furthermore, the complex bottom and rocky outcrops make such sampling techniques ineffective or impossible in many areas of the gulf.

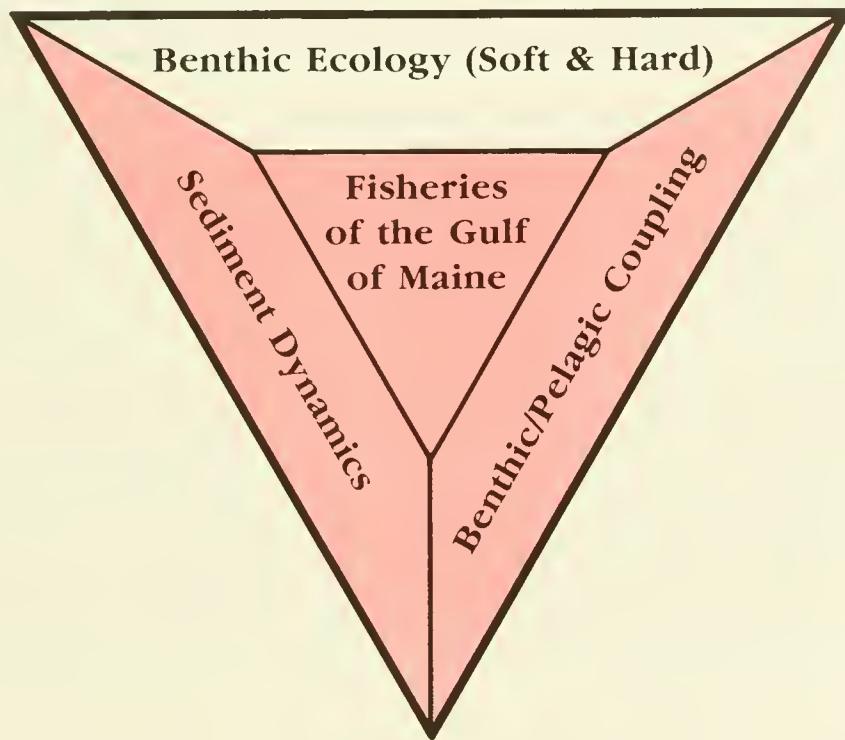
Manned undersea technology presents a unique opportunity to physically bring scientists to the benthos to study processes related to productivity in the gulf. Data collection on the

distribution and abundance of commercially important organisms, together with their ecology, is now possible. To understand the ecology of any species it is necessary to study its diet, habitat, behavior and the associated flora and fauna. Such studies must be site-specific and non-destructive and should include in situ manipulative experiments. Without submersibles such studies would be impossible. Much of the published data lack the resolution available using this undersea technology and is consequently unable to answer the questions we are posing.

The ultimate goal of the concerted research efforts seeks to understand what factors control the carrying capacity of fisheries-related organisms within the Gulf of Maine ecosystem, which in turn contributes to the economic and biological carrying capacity of the regional human population. This volume presents the first results of the studies of the benthic productivity and traces energy transfer from primary productivity to higher trophic levels. The organization of the volume roughly mirrors this flow with chapters dedicated to each session presented at the undersea science symposium held at the University of Connecticut at Avery Point in October, 1987. To illustrate this, the logo appearing at the beginning of this volume serves to identify topics under each research section. The logo is designed to illustrate the interrelationships that exist between each section. Some studies could just as easily been placed in a different section. Each chapter in this volume is prefaced by a summary of the papers and a report of the current status of research in each section.

Chapter one, BENTHIC ECOLOGY - HARD SUBSTRATA examines a unique rock-dwelling community centrally located in the gulf and what appears to be a distinctly different food web that exists there. Chapter two, BENTHIC ECOLOGY - SOFT SUBSTRATA focuses on the most abundant organisms found throughout the gulf. Chapter three, SEDIMENT DYNAMICS examines the horizontal transport and composition of sediments at several coastal and central gulf locations. Sediment studies involve both those concerned with grain size (ranging from boulders to micrometer size particles) and origin (i.e., inorganic sand to organic shell hash and nepheloid or "fluff" layers). Aspects of vertical transport of constituent particles is the focus of chapter four, BENTHIC-PELAGIC COUPLING. Benthic-pelagic coupling refers to the linkage between processes occurring in the water column and on the benthos. This involves not only particle distribution and productivity raining from the water column but also the reverse in the form of benthic resuspension of sediments and biotically-mediated upward transport of organics. Chapter five, FISHERIES examines the relationship between scallops and groundfishes and their habitat and prey. A herring egg bed study is also the focus of site-specific research.

Benthic Ecology—Hard Substrata



SESSION SUMMARY: BENTHIC ECOLOGY - HARD SUBSTRATA

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Rock outcrops along the shores and scattered throughout the Gulf of Maine contribute to its high habitat diversity and productivity. Because productivity, abundance and diversity of rock-dwelling organisms is greater (per unit area) than it is for other habitats, research on their ecology will allow more realistic estimates to be made of total productivity, carrying capacity, and food webs of the Gulf of Maine.

Research on hard substratum habitats targeted an offshore site at Ammen Rock Pinnacle (part of the Cashes Ledge complex) which is centrally located in the Gulf. Communities there are unique in species composition, abundance of organisms (including commercially important finfishes) and the nature of their food webs. Specifically, they provide us with a rare opportunity to study benthic primary productivity in a region isolated from coastal habitats which are affected by intense herbivory and variable nutrient inputs from terrestrial runoff and tidal mixing. They also allow us to conduct research on a benthic community dominated by fish rather than the invertebrate predators that characterize coastal habitats throughout the Gulf of Maine. NURP support of manned submersibles and scuba diving operations have allowed protracted and wide-ranging manipulative studies to be conducted on these deep water rock assemblages. Such studies, together with extensive research in shallower coastal habitats allow comparisons to be made of the patterns, processes and mechanisms structuring nearshore vs offshore communities.

The research at Ammen Rock Pinnacle and other offshore sites is very much "in progress". The strategy has been to quantify patterns in the distribution and abundance of benthic organisms and their predators and then to focus on the processes such as recruitment, productivity, growth, competition and predation important to the observed patterns. The paper of Vadas and Steneck reports on the zonation pattern of deep water algal populations on Ammen Rock Pinnacle where three distinct zones of dominance appear at various depths, each with distinct morphologies. Witman and Sebens studied patterns of benthic invertebrates, predators and aspects of the local physical oceanography. These two teams have been collaborating in NURP-UCAP sponsored submersible projects in this area over past four years. This collaboration has grown this year to include joint projects on kelp competition and fish predation.

The algal assemblage discovered at Ammen Rock Pinnacle is one of the deepest in the world for a cold water habitat and contains undescribed species. So far the research of Vadas and Steneck indicate that primary production at great depth may be higher than previously expected, and thus, offshore ledges may be a trophic oasis in a relative nutrient desert. Manipulative experiments (initiated in 1985) in which algae was transplanted along a depth gradient, are beginning to yield the first information of recruitment, survivorship, growth and primary production in this type of habitat. Steneck and Vadas are now focussing their attention on the processes of algal settlement and recruitment. Ian Davison and coworkers used reciprocal transplants and laboratory studies in 1987 to demonstrate that there are specific and possibly genetically fixed adaptations to living in deep water.

Witman and Sebens have quantified patterns of distribution and abundance of benthic invertebrates along a depth gradient on the same transect studied by Steneck and Vadas. Rates of secondary, and tertiary (predators of sessile invertebrates) production are being assessed by studying multiyear experiments. Those experiments were designed to determine rates of recruitment, growth, predation and survivorship along a depth gradient from 30 to 75 m. Some of the abundant and commercially important cod, pollock, cusk, haddock, and wolffish were observed feeding on the bottom. Feeding rates and food selection of those fishes have been studied using time-lapse movies and manipulative studies. Aspects of fish predation are being studied collaboratively with the team of Vadas and Steneck. A new area of research initiated by Witman and Sebens in 1986 was to examine the flow characteristics of water overlying their study sites as potential mechanism for food transport for a variety of sessile benthic invertebrates.

The result of the combined studies of Vadas and Steneck and Witman and Sebens is to determine the distribution and abundance of rock dwelling organisms on offshore ledges and to establish the nature of local food webs, energy flux, and carrying capacity of these ecosystems as important components of the Gulf of Maine. During the course of the project described above, several significant discoveries were made. Some species such as sea urchins, which are abundant in coastal habitats, are absent at this site. Their absence and the rarity of decapods (crabs and lobsters) may be due to predation on them by large, commercially-important fishes. Other organisms such as certain encrusting algae, crinoids and Metridium anemones are more abundant than previously reported for coastal habitats in the western North Atlantic. Possibly the most significant finds are the kelp, sponge, and limpet species which have never-before been reported for North America. Studies of chloroplast DNA indicate that the kelp is an undescribed species. It is possible that we have discovered a species assemblage unique to the central Gulf of Maine. This is the only region in the Gulf where cold "Maine Intermediate Water" contacts hard substrata within the

photic zone. Possibly because of the thermal attributes of the Maine Intermediate Water, some aspects of this biota are similar to that of northern Europe. The significance of such findings may be to contribute to solving long-standing debates over what controls biogeographic differences on opposite coasts of the Atlantic. In sum, the localized site-specific studies being conducted on rock substrata in the central Gulf of Maine may ultimately have much broader implications concerning biogeography, the structure of benthic communities, their energy flow and the impact of vertebrate predators on these communities.

DEEP WATER BENTHIC ALGAL
ZONATION IN THE GULF OF MAINE

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ABSTRACT

Algal community structure is described for a deep-water rock pinnacle in the Gulf of Maine. Three depth zones of algal dominance are apparent and consist of 1) leathery macrophytes (to 40 m), 2) foliose red algae (to 50 m) and 3) crustose algae (fleshy crusts to 55 m and coralline crusts to 63 m). Microscopic filamentous and erect calcareous algae are also present but inconspicuous. Upright macroscopic filamentous and thin sheet-like forms were not observed on the pinnacle. Sea anemones (Metridium senile) dominate some vertical faces and abrupt prominences in the shallowest regions of the pinnacle (to 24 m) and locally appear to set the upper vertical limits of kelp and possibly foliose reds. Laminaria sp. forms an open park-like canopy from 24 to 30 m whereas Agarum cibrosom the deepest kelp, grows as isolated individuals to 40 m. Peyssonnelia sp. and Leptophytum laeve are the deepest occurring fleshy and calcareous crusts, respectively. The occurrence of these algae at record depths for the Gulf of Maine and for cold water marine environments may be the result of an absence of large herbivores and the high productivity potential of the benthos in these relatively clear waters. By compiling data on depth distribution patterns world wide, it is evident that the three zone structure of algal morphologies observed in the Gulf of Maine is a global phenomenon.

INTRODUCTION

Globally, marine plants account for most of the primary production on earth. In many productive coastal regions, a significant portion of the production is from attached macroalgae (Mann, 1973). The vertical limit of this production, however, is restricted to relatively shallow depths which differ from place to place depending on oceanographic conditions. To assess the potential contribution of benthic macroalgae to global marine productivity, we need to know the depth limits or extinction depths (sensu Sears and Cooper, 1978) of these plants. Although research has been conducted on extinction depths of tropical plants, relatively few studies exist for cold water habitats.

In the past decade the use of scuba, manned submersibles,

and remote video devices has extended our knowledge of depth maxima of algal communities significantly (summarized in Table 1). These include discoveries of record extinction depths for the tropical Atlantic (Littler et al., 1985, 1986) and tropical Pacific oceans (Agegan and Abbott, 1985) and the unique deep water kelp communities of the Mediterranean Sea (Mojo and Buto, 1970; Drew et al., 1982). Overall, however, patterns of extinction depth distribution of algae are rare, or spuriously collected, depending on the availability of deep diving submersibles or manned underwater habitats (Earle, 1972; Sears and Cooper, 1978; Littler et al., 1986). Although other deep water collections have been reported, we have not listed them because they represent dredged specimens, (e.g., Laminaria brasiliensis is reported from depths greater than 70 m; Joly and Oliveira Filho, 1967; Oliveira Filho, 1976).

Light is often considered to be the most important element influencing patterns of algal depth distributions. This was recently reviewed by Hiscock (1986, p. 294) who stated:

"Several studies, including those published by Boulter et al. (1974), Norton et al. (1977) and Luning and Dring (1979), have indicated that the critical depth below which kelp fail to grow is where about 1% of surface illumination is reached. For the foliose red algae, the critical depth is that at which c. 0.1% of surface illumination penetrates."

Hiscock's (1986) review indicated that algal extinction depths are constant for kelp and foliose algae when considered as a function of the percentage of surface irradiance. This suggestion has not been tested in the western North Atlantic which contains a different subtidal algal flora.

What little is known of algal depth patterns in the western North Atlantic Ocean has been described largely from nearshore scuba observations (Lamb and Zimmerman, 1964; Edelstein et al., 1969; Adey, 1973; Sears and Wilce, 1975; Steneck, 1978; Mathieson, 1979; Himmelman, 1980; Mathieson et al., 1981). Relatively few direct observations have been made subtidally on offshore islands or submerged ledges (but see Sears and Cooper, 1978). These offshore habitats are important to study, however, because their geographic isolation and oceanic character make them unique. Additionally they may provide insight into processes such as recruitment, productivity, herbivory and evolutionary relationships which are important to more broadly distributed nearshore communities.

Here we describe the algal assemblage of a submerged pinnacle that lies well offshore in the Gulf of Maine and has a relatively shallow (24m) summit. We report several new depth records for the North Atlantic, the existence of a deep water Laminaria "park" (sensu Kitching, 1941) and a three zone depth pattern of algal dominance which we believe may be a worldwide

TABLE I
Summary of benthic algal depth maxima for various biogeographic provinces.

CITATION	LOCATION	BIOGEOGRAPHIC PROVINCE	ALGAL SPECIES OR FORM	DEPTH (M)
Lang 1974	Jamaica	TROPICS	Crustose red and filamentous green	175
James & Ginsburg 1979	Glovers reef	Tropical Caribbean	Crustose coralline	250
		Tropical Caribbean		
Littler et al. 1985	Bahamas	SUBTROPICS	" <i>Lithothamnia</i> "	175
Littler et al. 1985	San Salvadore		Crustose coralline	268
Littler et al. 1985	San Salvadore		<i>Ostreobium</i>	210
Littler et al. 1985	San Salvadore		<i>Peysonnelia</i>	189
Littler et al. 1985	San Salvadore		Johnson-Sealinkle profunda	157
Littler et al. 1985	San Salvadore		<i>Halimeda copiosa</i>	130
Littler et al. 1985	San Salvadore		<i>Lobophora variegata</i>	88
Littler et al. 1985	San Salvadore		Foliose seaweeds	100
Taylor 1928	Florida		Foliose algae	200
	Hawaii		Crustose coralline	366
	Florida	Subtropical N. Atlantic	Syringoderma	90
Molinier 1960ab	Corsica	MEDITERRANEAN	" <i>Lithothamnia</i> "	120
Drew 1969	Maltese archipelago		Varied	75
Mojo & Buta 1971	Straits of Messina		<i>Laminaria</i>	95
Giaccone, 1972	Straits of Messina		<i>Laminaria</i> and others	25
Fredj 1972	Corsica		<i>Laminaria rodriquezii</i>	95
Fredj 1972	Corsica		" <i>Lithothamnia</i> "	120
Drew 1974	Straits of Messina		<i>Laminaria</i>	55
Drew et al. 1982	Straits of Messina		<i>Laminaria</i>	55
Boutler et al. 1974	Roscoff	BOREAL-TEMPERATE	<i>Laminaria hyperborea</i>	25
Ernst 1966	Bretagne		<i>Laminaria hyperborea</i>	30
Kain 1971	Isle of Man		<i>Laminaria hyperborea</i>	20
Castric-Fey et al. 1973	de Glenan Archipeligo		<i>Laminaria hyperborea</i>	30
Castric-Fey et al. 1973	de Glenan Archipeligo		<i>Laminaria hyperborea</i>	47
Kain 1976	British Isles		Various algae	24
Kain 1971	Isle of Man		<i>Laminaria hyperborea</i>	19
Luning & Dring 1979	Helgoland		<i>Laminaria hyperborea</i>	8

Maggs & Guiry 1982	Ireland	Boreal E.	Atlantic	<i>Laminaria hyperborea</i>	32
Cullinane & Whelan 1983	Ireland	Boreal E.	Atlantic	<i>Laminaria hyperborea</i>	22
Cullinane & Whelan 1983	Ireland	Boreal E.	Atlantic	<i>Delesseria sanguinea</i>	27
Jorde 1966	Bergen Norway	Boreal E.	Atlantic	<i>Laminaria hyperborea</i>	30
SUBARCTIC					
Lamb & Zimmermann 1964	Cape Ann, MA	Subarctic W.	Atlantic	<i>Laminaria</i>	12
Lamb & Zimmermann 1964	Cape Ann, MA	Subarctic W.	Atlantic	<i>Foliose Reds</i>	20
Sears & Cooper 1978	Gulf of Maine	Subarctic W.	Atlantic	<i>Foliose Red Algae</i>	38
Sears & Cooper 1978	Gulf of Maine	Subarctic W.	Atlantic	<i>Crustose Corallines</i>	47
Mathieson 1979	Gulf of Maine	Subarctic W.	Atlantic	<i>Crustose Corallines</i>	24
Mathieson et al. 1981	Gulf of Maine	Subarctic W.	Atlantic	<i>Laminaria</i> spp.	18
Mathieson 1979	Gulf of Maine	Subarctic W.	Atlantic	<i>Crustose and filamentous algae</i>	32
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>L. longicruris</i>	30
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>L. solidungula</i>	40
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Lithothamnion tophiforme</i>	40
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Phymatolithon laevigatum</i>	37
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Phyllophora</i>	25
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Agarum cribosum</i>	25
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Turnerella pennyi</i>	30
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Lithothamnion galactiale</i>	30
South 1983	Georges Bank	Subarctic W.	Atlantic	<i>Ptilota serrata</i>	30
South 1983	Gulf of Maine	Subarctic W.	Atlantic	<i>Peysonnelia</i>	30
South 1983	Gulf of Maine	Subarctic W.	Atlantic	<i>Foliose Red Algae</i>	48
Sears in Press	Gulf of Maine	Subarctic W.	Atlantic	<i>Crustose Coralline</i>	53
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Laminaria longicruris</i>	30
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Laminaria</i> sp.	35
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Agarum cribosum</i>	40
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Foliose reds</i>	50
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Algal crusts</i>	63

phenomenon. An interesting and important feature of the Ammen Rock site is the lack of large herbivores, especially sea urchins, which may contribute to the establishment and persistence of these macroalgal assemblages at record depths.

MATERIALS AND METHODS

During the summers of 1984 and 1985 we made a series of dives with the 2-man submersible, Mermaid II, 4-man submersible Johnson Sea-Link and an unmanned reconnaissance vehicle, Recon IV, as a part of NOAA's National Undersea Research Program. We report here on the results of two Recon IV surveys and four Mermaid II and Johnson Sea-Link dives on a shallow pinnacle (ca 24 m) near Ammen Rock which is part of Cashes Ledge approximately 104 km east of Boothbay Harbor, Maine (Fig. 1).

Our study site, called "Ammen Rock Pinnacle" is located in the center of the Gulf of Maine and is influenced by strong currents and oceanic water masses of low turbidity (we observed up to 30 m lateral visibility, see also light data below) and high salinity. Water temperatures from June to August are typical for Maine Intermediate Water (Hopkins and Garfield, 1979) and ranged from 5°C to 9°C at the summit of the pinnacle and from 5°C to 6.5°C at 75 m. Typically however, benthic temperatures ranged from 5.5°C to 7.5°C in the photic zone. The Ammen Rock Pinnacle consists of a steeply sloping granitic outcrop. The walls descend sharply from the summit to about 30 m and then at a lesser angle to 43 m. Large boulders lie at the base of the pinnacle forming a talus slope. Below 43 m, boulders and ledge outcrops form most of the available hard substrata, gradually being replaced by cobbles rocks, sand and small outcrops of ledge. Sediment accumulations increase with depth and increasingly reduce the amount of primary substratum on horizontal surfaces below 50 m.

Visual (recorded with cassette tape), photographic and video observations were made on the submersible dives. The submersibles were equipped for limited collecting with a suction sampler and a manipulator arm. Neither collection technique was satisfactory but between them provided voucher specimens or fragments of several algae. Rocks encrusted with coralline algae up to 30 x 30 cm in size were collected with the manipulator arm. During 1985 limited scuba diving was permitted to 30 m to collect algae. Underwater light readings were made in 1985 by Dr. James Sears with a Licor Underwater Photometer Model Li 185B with a cosine corrected sensor. The unit measures PAR in the 400-700 nm waveband and the unit of measurement is u. A series of 5 tests were run over a two day period at midday during calm clear weather conditions. For comparison a similar test was run with a Licor Model 188b integrating quantum meter with a Li 905B spherical sensor during calm conditions on the coast at Pemaquid, Maine.

Data records of algal observations were pooled from our

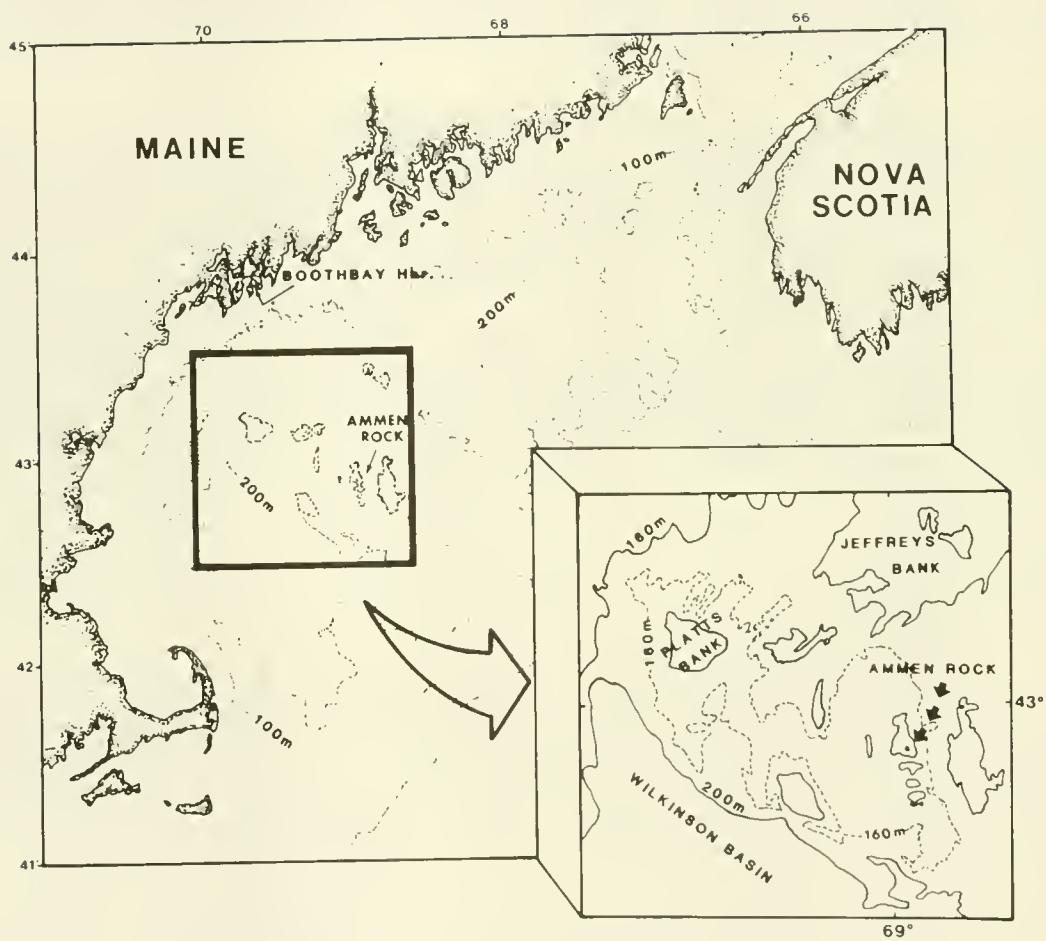


Figure 1. Location of study site at Ammen Rock Pinnacle in the Gulf of Maine.

observations and those made by J. Sears, K. Sebens and J. Witman.

RESULTS

Seventeen algal species were recorded from Ammen Rock Pinnacle including three kelps, five foliose reds, two small filamentous forms, three fleshy red crusts, three crustose corallines and one erect articulated calcareous alga (Table 2). Surprisingly, large filamentous and thin sheet-like algae were not observed on the pinnacle. All of the specimens observed or collected at these depths appeared healthy and several were reproductive. Interestingly, the thallus sizes of kelps were sharply truncated at the deepest depths. Typically the maximum size of thalli for each taxon decreases with depth. Kelps, for example, ranged in size from 100-200 cm near the summit to 10-20 cm at the lowermost limits.

A striking zonation pattern exists on the pinnacle (Fig. 2). The summit of one of the shallower peaks (observed in 1984 but not located in 1985) was not examined in detail but the upper walls (ca 23m) were covered by dense carpets of sea anemones, Metridium senile. Kelps began at 24m and co-occurred with sea anemones over much of their range to a depth of 40m. Foliose red algae grew in the kelp zone and extended to a depth of 50m. Corallina officinalis was observed at 24 to 30m whereas calcified (coralline) and non-calcified (fleshy) algal crusts were observed at all zones having algae. Peyssonnelia was the deepest occurring fleshy crust (55 m) whereas Leptophyllum laeve was the deepest coralline crust and alga observed on the pinnacle (63m).

Invertebrate populations were also zoned with depth. Below the shallow band of M. senile from 50-90m were patchy assemblages of sponges (Haliclona, Suberitechinus, Polymastia, and Phakellia), ascidians (Aplidium, Ascidia, and Botrylloides), and two other anemones (Tealia and Bolocera). Also invertebrates such as Modiolus and Myxicola were abundant in places at this depth range. Most conspicuous in their absence within the zones of algae were sea urchins. All other herbivores were rare. We collected a few small limpets and chitons but these would have little impact on benthic algae.

The kelp zone was occasionally sandwiched in places between dense beds of Metridium. The dominant kelp was a Laminaria species of uncertain taxonomic affinity but which resembles L. digitata. The great depths to which this species grows, aspects of its morphology (described below) and anatomy (presence of mucilage ducts in the frond and stipe) suggest that this may be a new taxon. This Laminaria formed an open or park-like canopy (sensu Kitching, 1941; Luning and Dring, 1979) mainly between 25-30m. Individual stipes were spaced 0.2 to 0.5 m apart. Fronds of this species were up to 2m in length with wide, sparsely digitate lamina with one or two conspicuous vertical constrictions. The latter apparently occur annually suggesting that the larger fronds survive for a

TABLE 2

DEPTH RANGES AND REPRODUCTIVE PATTERNS OF
ALGAE AT AMMEN ROCK PINNACLE

<u>Species</u>	<u>Depth Range & Maxima</u> ¹	<u>Reproductive Condition</u> ²
LEATHERY MACROPHYTE ASSEMBLAGE (To 40 M)		
<u>Agarum cibrosum</u> (Mertens) Bory	24-33*-40 M	MS
<u>Laminaria longicruris</u> De la Pylaie	24-30*	NR
<u>Laminaria</u> sp. Lamouroux	24-27*-35	NR
FILAMENTOUS ASSEMBLAGE (To 33 M)		
<u>Audouinella purpurea</u> (Lightfoot) Woelkerling	24-33*	NR
<u>Uronema curvata</u> Printz	24-33*	NR
FOLIOSE ASSEMBLAGE (To 50 M)		
<u>Callophyllis cristata</u> (C. Agardh) Kutz	24-33*-40	CS
<u>Membranoptera alata</u> (Hudson) Stackhouse	24-33*-40	CS
<u>Phyllophora truncata</u> (Pallas) A. Zinova	40	
<u>Phycodrys rubens</u> (Linnaeus) Batters	24-33*-50	NR
<u>Ptilota serrata</u> Kutz	24-33*-50	CS
ARTICULATED CALCIFIED ASSEMBLAGE (To 33 M)		
<u>Corallina officinalis</u> Linnaeus	24-33*	C
CRUSTOSE ASSEMBLAGE		
Non-calcified forms (To 55 M)		
<u>Petrocelis</u> sp. ³	30-43*	NR
<u>Peyssonnelia</u> sp. ⁴ Decaisne	30-55*	NR
<u>Cruoriopsis</u> sp. ⁴	43*	NR
Calcified forms (To 63 M)		
<u>Leptophytum laeve</u> (Stroemfelt) Adey	24-61*-63	TS (61M)
<u>Lithophyllum orbiculatum</u> (Foslie) Foslie	24-43*	TS (30M)
		43
<u>Lithothamnium lemoineae</u> Adey	24-49*	NR

1) *Indicates species identified from collected specimens. Depth ranges of species without an asterisk were determined visually or from video.

2) NR=Not reproductive, MS=Meiosporic, CS=Cystocarpic, TS=Tetrasporic.

3) This may be the alternate stage for Gigartina.

4) This may be the alternate stage for Gloiosiphonia.

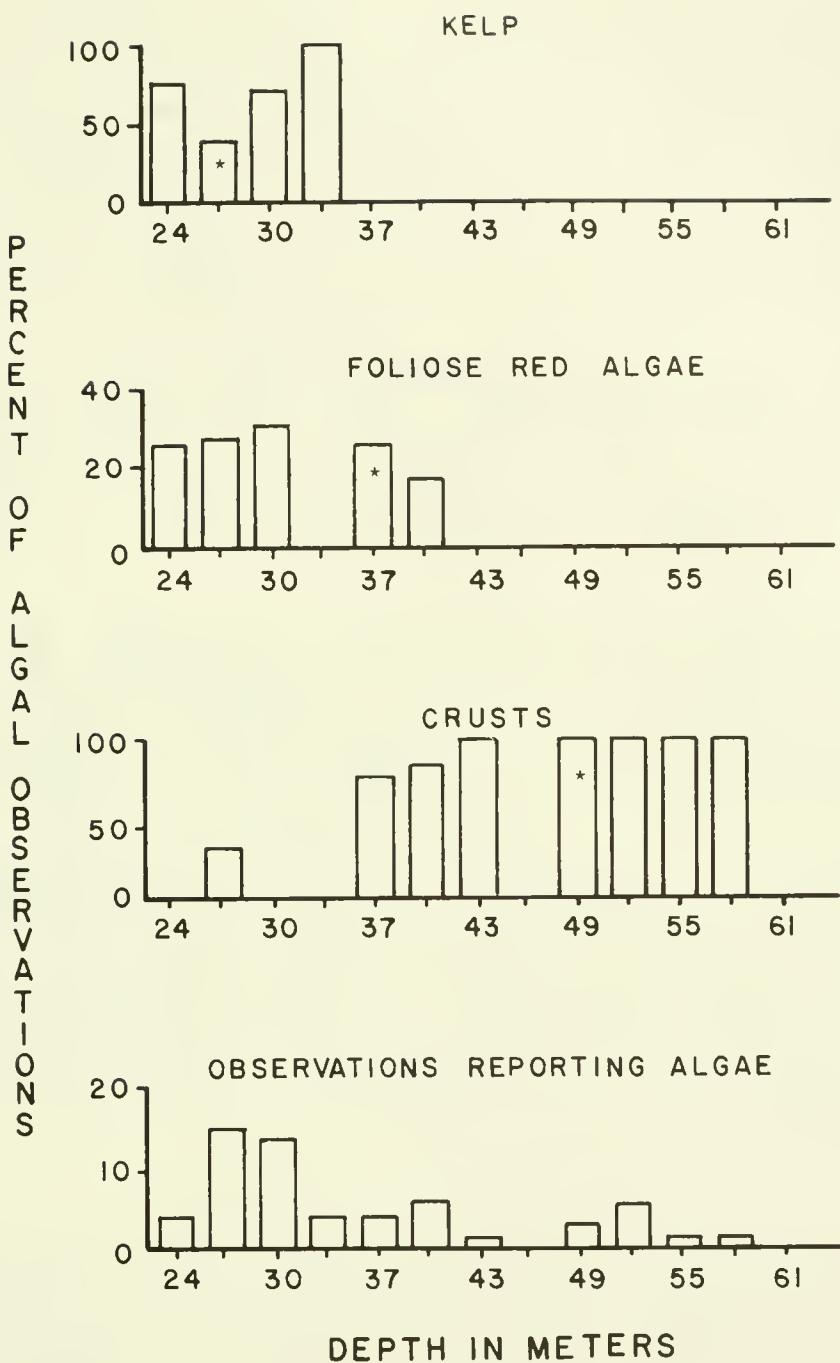


Figure 2. Relative abundances of major algal assemblages at Ammen Rock Pinnacle as a function of depth (species listed in Table 1). Abundances were determined by counting the frequency of all observations during 1984 (Recon IV and Mermaid II study). Asterisk indicates a depth where an algal assemblage was reported to be dominant (> 50% cover).

period of 2 to 3 years. The structure of the holdfast also appears to support this interpretation, which usually shows two to three (occasionally seven) distinct whorls of haptera. Locally, we observed a striking pattern of broad clear areas surrounding many of the Laminaria plants. These halos presumably were due to whiplash effects from the long sweeping fronds. Agarum cribrosum was the deepest recorded kelp (40m), although small non-digitate plants resembling the genus Laminaria were also observed in the same zone (35-40m) but could not be collected. Laminaria longicruris was extremely rare and interspersed with Laminaria sp. at the shallower depths.

Foliose red algae were dispersed among kelp and on ridges between dense stands of anemones where they formed narrow dense patches. They also occurred singly or as tiny, inconspicuous tufts. Dominant in this assemblage was Ptilota serrata and Phycodrys rubens (about equally abundant). We also found Callophyllis cristata, Membranoptera alata and Phyllophora truncata (Table 2).

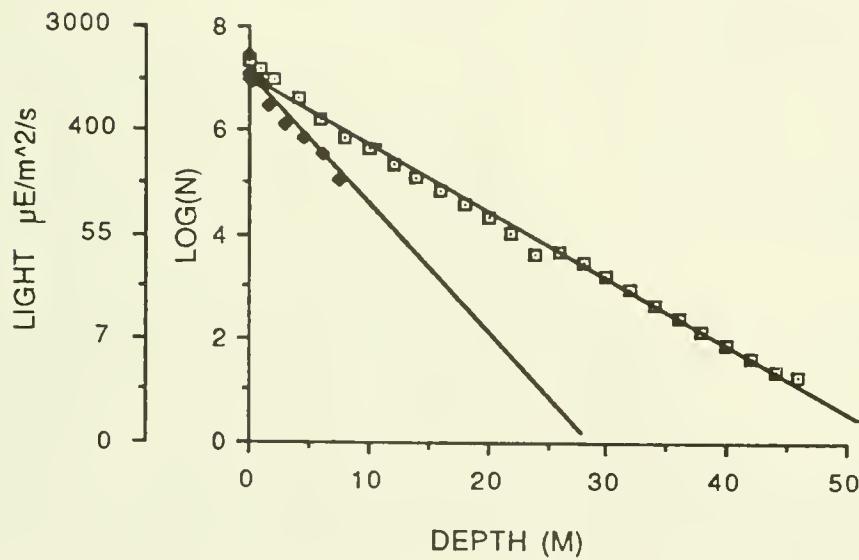
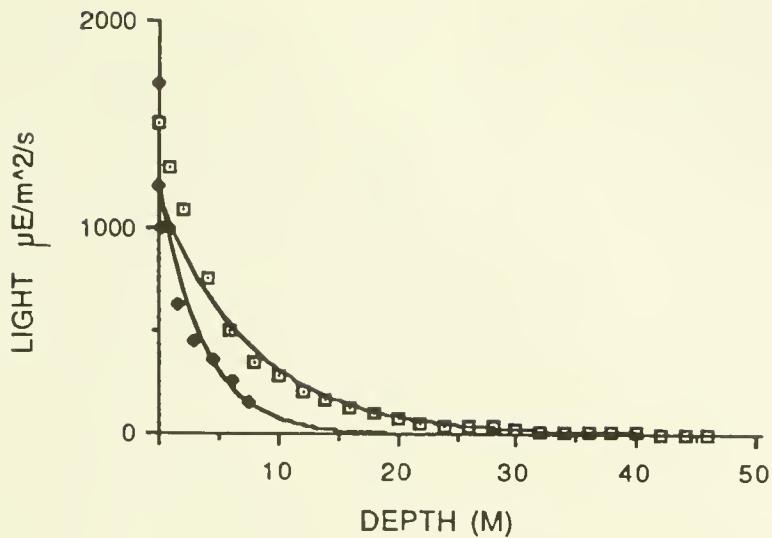
Both calcified and noncalcified crusts were found in all zones. Fleshy crusts are found slightly shallower (to 55m) than are coralline crusts (to 63 m) (Table 2). Coralline abundance was considerable at depths over 50 meters and was observed to cover up to 80% of the rock substrate in places. The dominant fleshy crust was Peyssonnelia and the dominant coralline crusts were Lithophyllum orbiculatum at 30 m and Leptophytum laeve at 55-63 m.

Underwater light readings revealed marked differences between Ammen Rock Pinnacle and the coast of Maine due to the turbidity of the water (Fig. 3). Both profiles approximate a linear function when natural log-transformed and show that light penetration at Ammen Rock is significantly greater. When expressed as percent of surface irradiance the light levels corresponding to the extinction depths of the three major functional-form groups are: 0.44% for kelps, 0.11% for foliose red algae and 0.02% for coralline crusts.

DISCUSSION

We found three distinct algal assemblages zoned with depth at the Ammen Rock Pinnacle. This pattern is not unlike those found in shallower nearshore regions throughout the Gulf of Maine and elsewhere. The patterns are recognizable as assemblages of morphologically similar species which represent distinct functional groups (sensu Littler and Littler, 1980; Steneck and Watling, 1982). Three of these groups; leathery macrophytes, foliose algae and crustose algae dominate the three depth zones respectively (Fig. 2).

The maximum depth for each of the three algal zones exceeds that known for the Gulf of Maine and for any boreal-subarctic environment (Table 1 and Fig. 4). This is probably due to the



◻ Ammen Rock Pinnacle 4 July 1985

◆ Pemaquid Point, Me. 25 July 1980

Figure 3. Light attenuation in coastal (Pemaquid Point, Me.) and offshore (Ammen Rock Pinnacle) habitats. Upper graphs are untransformed data with regressions of $y = 1218 \times 10^{(-0.12x)}$, $R = 0.98$ for Ammen Rock Pinnacle and $y = 1148 \times 10^{(-0.06x)}$, $R = 1.00$ for Pemaquid Point, Me. Lower graphs are natural log transformed data with regressions of $y = 7.0 - 0.13x$, $R = 1.00$ for Ammen Rock Pinnacle and $y = 7.1 - 0.27x$ $R = 0.98$ for Pemaquid Point, Me.

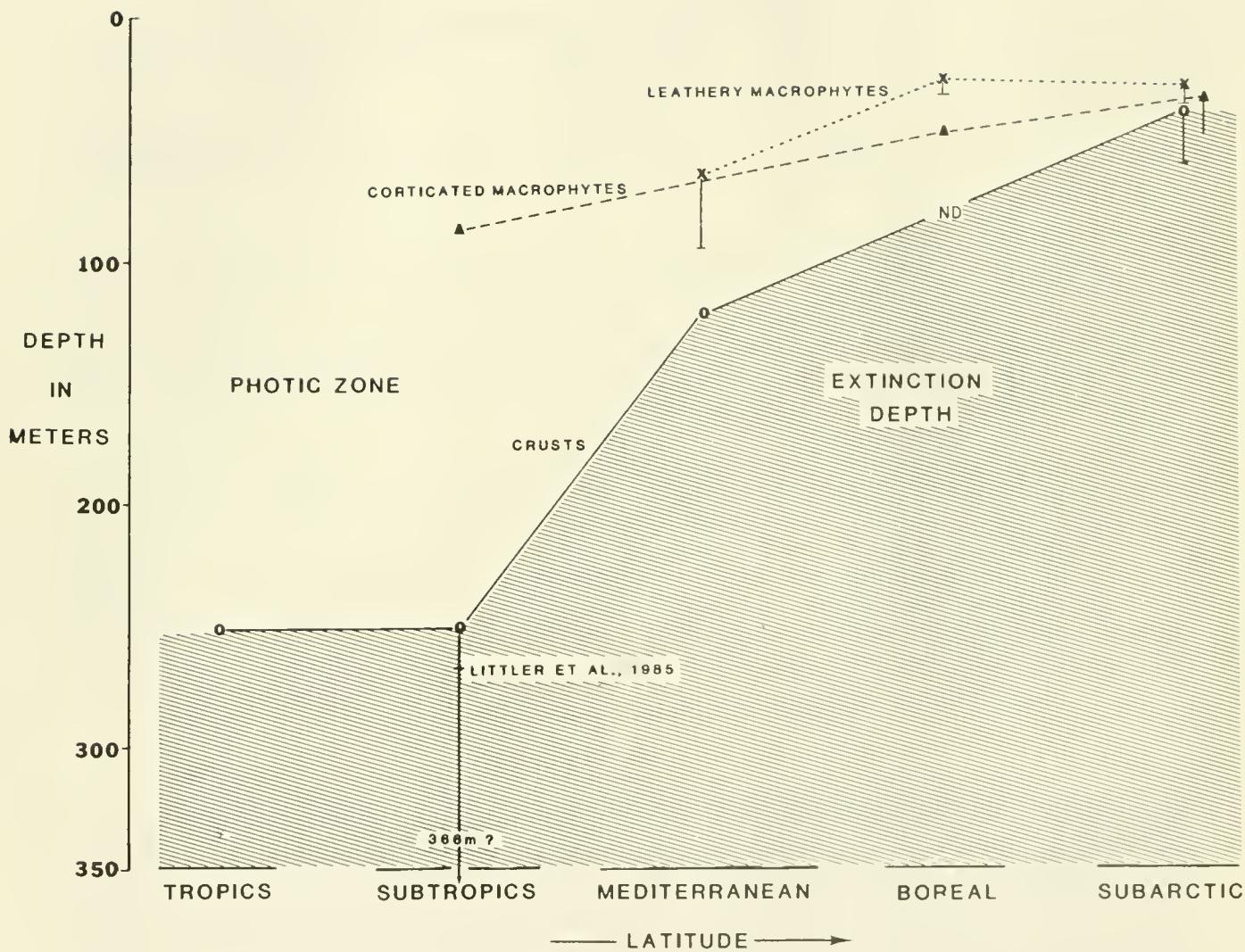


Figure 4. Biogeographical depth patterns for these algal functional groups (based on literature cited in Table 1 and this study).

clarity of water and absence of herbivores at Ammen Rock Pinnacle. Both factors are important but light levels undoubtedly are more important at this site. Although extinction depths vary greatly depending on water clarity, traditionally the percent of surface illumination correlating with algal depth limits is thought to remain rather constant (Hiscock, 1986). Our data conforms with other published studies for algal crusts (.02% of surface illumination, Sears, 1987 but see Luning and Dring, 1979; Hiscock, 1986), and foliose algae (.1% of surface illumination, Luning and Dring, 1979; Hiscock, 1986; Sears 1987). However, we found kelp growing at significantly lower light levels (0.44%) than previously reported (0.7% Luning and Dring, 1979 and Sears, 1987; 1% Hiscock, 1986). Littler et al. (1985), however, observed lower light intensities for tropical algae (.05% foliose algae, .0005% crustose corallines). Thus percent surface illumination may provide a good rule of thumb for certain regions and forms but the values are not absolute.

Although the depth maxima of algae are set by light, the virtual absence of herbivores from the pinnacle is significant. Sea urchins are dominant structuring forces in much of the Northwest Atlantic (Breen and Mann, 1976) and Gulf of Maine (Sebens, 1985; Witman, 1985; Vadas et al., 1986). The causes for their absence from the pinnacle is unknown, although preliminary experiments suggest predation from fishes is involved (Steneck and Vadas, unpublished data). Nonetheless it is the absence of herbivores that allows the presumed physiological depth limits of these fleshy algae to be expressed.

Another unusual feature is the local dominance of anemone patches (*M. senile*) on vertical rock walls and prominences near the summit of the pinnacle. In part this may be due to the formation of dense mats (possibly clones) on most shallow outcrops. Clonal development in marine organisms is an effective strategy for occupying primary space in the subtidal zone (Jackson 1979) and thus competition may be preventing locally the extension of kelps and other algal groups into these patches.

There is a clear pattern in the zonation of algal species and functional groups on the pinnacle. Both species and functional group diversity is greatest at the shallowest depths. The successive loss with depth of leathery macrophytes, corticated macrophytes, noncalcified crusts and finally calcified crusts seen at Ammen Rock Pinnacle (Fig. 2, Table 2) is also a global phenomenon (Table 1, Fig. 4). Although it has long been recognized that shallow zones dominated by large leathery macrophytes also have a diverse understory of species and other functional groups such as, corticated macrophytes, foliose, filamentous and crustose forms (Dawson et al., 1960, Neushul, 1967), the universality of this subtidal zonation pattern at a functional group level has gone unrecognized. Lamb and Zimmerman (1964) and Neushul (1967) recognized a tripartite pattern of zonation but these zones were identified by the dominant species not morphologies. For example, they identified

shallow Laminaria zone, a deeper Agarum zone and a diverse assemblage of two or three functional groups in the deepest zone. Other studies on subtidal zonation have correlated differences in pigment composition ("chromatic adaptation") with depth such that from shallow to deep water: brown, green and red algae (Larkum et al., 1967; Dring, 1981; Littler et al., 1986) are said to dominate respectively. Interestingly at Ammen Rock Pinnacle, there is no green zone, the brown zone is compressed and the red zone exists over the entire vertical range of algae. Although our site may be too deep for a green zone, the zonation pattern appears to correspond more closely to morphological types than to pigmentation.

The repeating pattern of zonation at a functional group level begs the question: are these morphologies adaptive, and if they are what is it about them that allow certain forms to consistently dominate particular depth zones? Littler et al., (1986) have, in part, provided an answer, by showing that encrusting tropical deep water algae are photosynthetically two to three orders of magnitude more efficient than algae exposed to near surface light environments. This paper provides a first step in documenting the patterns in distribution and abundance for a temperate/boreal community - the processes controlling those patterns will require further study.

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COMPARATIVE PHOTOSYNTHETIC PHYSIOLOGY OF SHALLOW AND DEEP WATER
POPULATIONS OF LAMINARIA IN THE GULF OF MAINE

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INTRODUCTION

Previous research indicated the occurrence of a deep water population of Laminaria at Ammen rock and Ammen rock pinnacle in the central Gulf of Maine (Vadas and Steneck, 1988). The Ammen Laminaria closely resembles Laminaria digitata, which occurs through the North Atlantic including the coast of Maine. Ammen plants differ from coastal L. digitata by having narrower and less digitate blades, by possessing mucilage ducts in the stipe and holdfast and by the frequent occurrence of whorls of haptera in the holdfast. Furthermore, the Ammen Laminaria population occurs at considerable depth (25-35 m), whereas L. digitata typically has maximum abundance in shallow water. By themselves these differences are not sufficient to justify placing the Ammen Laminaria in a separate taxon from L. digitata. L. digitata is known to exhibit considerable phenotypic plasticity (Sundene, 1964) and the taxonomic significance of mucilage ducts is open to question (Chapman, 1973). However, recent preliminary studies indicate that large differences occur between chloroplast DNA sequences in Ammen Laminaria and coastal L. digitata (Fain, Vadas and Steneck, unpublished), suggesting that Ammen Laminaria may be a distinct species.

Thus, it is currently an open question as to whether or not the Ammen Laminaria is a new species, or if it is a deep water ecotype of L. digitata. Irrespective of the taxon to which the Ammen Laminaria population is eventually assigned, a key question is what, if any, adaptations have evolved for life in a deep water environment characterized by low light levels. *A priori* one would expect this population to have evolved adaptations to low irradiance because of the small size and extreme isolation of the population (Vadas and Steneck, 1988), which is continuously exposed to low light levels. In contrast, most coastal Laminaria populations are contiguous from shallow to deep water and hence experience a gradient of irradiance.

The objectives of the present study were to determine if the Ammen Laminaria population does possess specific adaptation to low light levels and to determine their nature. The experimental design involved a comparative study of the Ammen population with a

shallow water population of L. digitata. Because the physiological characteristics of the two populations will reflect both genetic differences and phenotypic acclimation to the light levels at the two sites, reciprocal transplants were performed in order that comparisons could be made between sporophytes from the two populations which had been exposed to similar irradiance levels. These experiments were performed during the summer 1987 curises of the RV Powell and RV Seward Johnson in the Gulf of Maine.

METHODS

Two populations were studied: a shallow water Laminaria digitata (Huds.) Lamour. population growing 1 m below mean low water at Thread-of-Life in Maine, and the Ammen population described previously (Vadas and Steneck, 1988) growing at 30 m at Ammen rock pinnacle. Initial samples were taken from these sites in late June 1987. 10 plants from each group were transplanted to each of three transplant sites: 1 m and 15 m at Pemaquid (a coastal site close to Thread-of-Life) and 30 m at Ammen rock pinnacle. Transplants had a blade length of between 30 and 60 cm. Plants were transplanted by opening the weave of short lengths of polypropylene rope to admit the holdfast and stipe of tagged plants. The polypropylene ropes were then attached to an anchored buoyed nylon line. Transplants at the coastal site were retrieved in late August 1987, immediately prior to the second cruise to Ammen rock. The 30 m Ammen transplants were retrieved in early September 1987. Plants were collected, and transplant manipulations performed, by SCUBA divers. Plants were transported between the two coastal and Ammen sites and to the laboratory at the University of Maine (Orono campus) in cold (5°C) seawater in large insulated coolers.

Growth of the transplanted Laminaria was monitored by the hole punch technique of Parke (1948). Five sporophytes were collected from each field site in June and taken to Orono for measurements of initial photosynthetic characteristics, activities of enzymes of carbon and nitrogen metabolism and biochemical analysis. Similar measurements were made on subsamples (n=5) of both plant groups after growth at the transplant sites. In the case of plants from the 1 and 15 m coastal sites these measurements were made at Orono, with the measurements on the 30 m Ammen transplants being made onboard the RV Seward Johnson.

Photosynthetic and respiratory measurements were made on 1.95 cm diameter discs punched from the blade 15-25 cm above the stipe-blade transition. Discs were held overnight (18 hr) in aerated seawater at 5°C and a photon flux density of 50 umole photons.m⁻².s⁻¹ in a 16:8 L:D photoperiod. This procedure allows wound healing to occur (Bidwell and McLachlan, 1985). Discs of L. digitata and Ammen Laminaria plants both release copious quantities of mucilage immediately after being cut. Discs were placed in the reaction chamber of a calibrated Rank oxygen

electrode together with 5 ml of millipore filtered (0.45 μ m pore size) seawater. Temperature was maintained at 15°C by a refrigerated thermostatic circulator connected to the water jacket of the electrode chamber. The output of the oxygen electrode was recorded on a strip chart recorder. The sensitivity of the measurements was increased by setting the chart recorder at 1 mV rather than 10 mV (the full scale output of the Rank electrode), offsetting the zero with a Baily RC-10 recorder calibrator.

The oxygen content of the filtered seawater was adjusted to 50-60% of saturation by sparging with nitrogen. Respiration rates were measured by enclosing the reaction chamber in a double layer of thick black cloth. Once a stable respiration rate was achieved the disc was illuminated with successively higher photon flux densities from 1.0 to 600 μ mole photons. \cdot m^{-2} . s^{-1} supplied by a slide projector. Photon flux densities were varied by means of Schott glass neutral density filters. Light levels were increased once a stable rate of oxygen flux was achieved at the previous photon flux density. The entire process took approximately 45-60 min. There was no evidence of photorespiration or nutrient limitation. Measurements were corrected for oxygen consumption by the electrode. Determinations were made on a single disc from each of 5 replicate plants.

Activities of the key Calvin cycle enzyme ribulose-1,5-bisphosphate carboxylase oxygenase (RUBISCO) and the key nitrogen assimilatory enzyme nitrate reductase (NR) were measured as described previously (Davison and Davison, 1987; Davison, 1987). Pigments were analyzed on discs used for photosynthesis measurements by extraction in DMSO and methanol as described by Seely et al. (1972). A further series of discs were extracted with hot 90% ethanol for the determination of mannitol, amino-N and NO_3^- as described previously (Davison and Davison, 1987).

Statistical analysis was performed on the data using 1 or 2 way ANOVA. Non-normal data was analyzed by ANOVA on data ranked using the Kruskal-Wallis procedure. Comparison of means was based on the Student Newman Keuls test. All statistical procedures were done using SAS version 5.16.

RESULTS

Growth rates of transplanted Ammen and coastal Laminaria are shown in Figure 1. Ammen plants transplanted to the 1 m coastal site grew significantly more slowly than coastal plants (0.082 vs 0.165 $cm\cdot mo^{-1}$, respectively). Ammen plants grew significantly faster at the 15 m site where both groups of plants achieved similar rates of growth (0.129 - 0.156 $cm\cdot mo^{-1}$). Coastal plants grew slowest (0.038 $cm\cdot mo^{-1}$) at the 30 m Ammen site. Although Ammen plants grew at 0.066 $cm\cdot mo^{-1}$ at the 30 m site there was no significant difference between the two groups of plants. However, when growth rates at this site were compared in terms of linear increase per month, significant differences were evident, with the

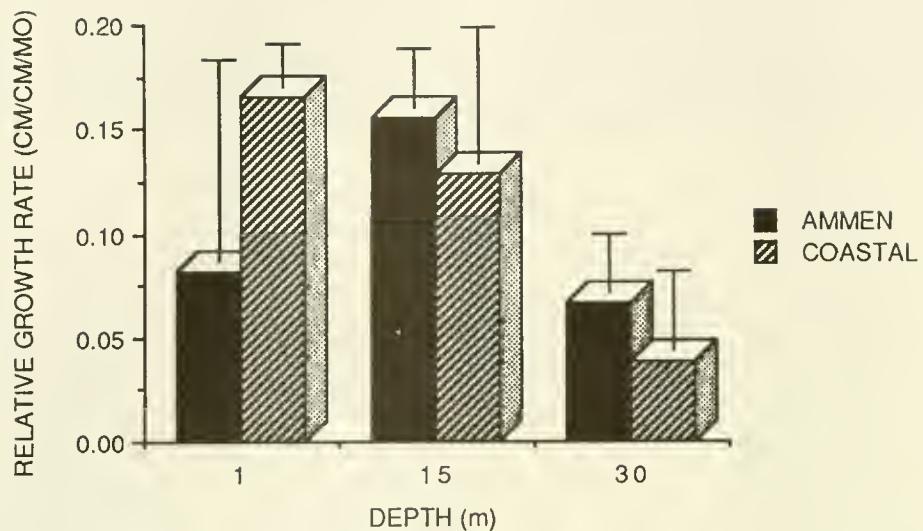


Figure 1. Relative growth rates of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

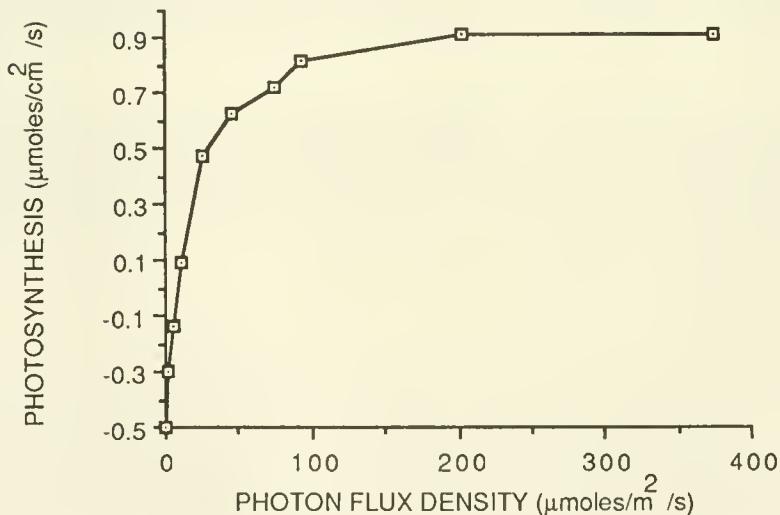


Figure 2. Representative data for photosynthesis versus irradiance response of coastal Laminaria digitata sampled June 1987.

Ammen plants increasing in length faster than the coastal group (4.38 vs 0.833 cm.mo⁻¹, respectively).

Figure 2 presents typical data for photosynthesis versus irradiance curves of coastal Laminaria digitata following the initial sampling of this population in June 1987. Similar curves were obtained for all groups of plants, although values for respiration, light compensation point, initial slope of the P vs I response (alpha) and light saturated rates of photosynthesis did vary between sites, and between plant group. These differences were compared by using the P vs I curves to calculate the following characteristics: respiration (umoles O₂. g f wt⁻¹.hr⁻¹): the mean oxygen consumption in the dark; alpha ([umoles O₂. g f wt⁻¹.hr⁻¹]/[umoles photons.m⁻².s⁻¹]): the slope of the initial, light limited region of the P vs I curve; P_{max} (umoles O₂. g f wt⁻¹.hr⁻¹): the average value of light saturated photosynthesis; I_k, the photon flux density required to just saturate photosynthesis (umoles photons.m⁻².s⁻¹): P_{max}/alpha; the light compensation point, where photosynthesis just balances respiration (umoles photons.m⁻².s⁻¹): calculated from alpha values and respiration rates.

Figure 3 presents data on the maximum rate of photosynthesis of the two groups of plants both initially and after growth at the three transplant sites. Initial P_{max} values were significantly greater for coastal Laminaria digitata than Ammen plants (0.806 vs 0.234 umoles.cm⁻².s⁻¹). The P_{max} of the coastal plants did not change significantly at any of the transplant sites. In contrast, Ammen plants transplanted to both the 1 and 15 m coastal sites and the 30 m Ammen site did exhibit considerable increases in P_{max} (to between 0.526 and 0.683 umoles.cm⁻².s⁻¹), although the rates were always lower than those of the coastal group.

Alpha values for the initial and transplanted plants are shown in Figure 4. Alpha values of coastal plants were significantly higher than those of the Ammen Laminaria in all cases except the 15 m coastal site. Alpha values were highest in the initial samples (0.052 and 0.035 [umole.cm⁻².hr⁻¹]/[umole photons.m⁻².s⁻¹] for coastal and Ammen plants, respectively) and lowest in the 30 m transplants (0.052 and 0.035 [umole.cm⁻².hr⁻¹]/[umole photons.m⁻².s⁻¹] for coastal and Ammen plants, respectively).

I_k values for photosynthesis are shown in Figure 5. There were no significant differences between the two groups of plants either initially or at any of the transplant sites. I_k values were lowest in the initial samples (7.21 and 15.60 umole photons.m⁻².s⁻¹ in Ammen and coastal plants, respectively) and highest at the 30 m transplant site (7.21 and 15.60 umole photons.m⁻².s⁻¹ in Ammen and coastal plants, respectively).

Figure 6 shows data for the light compensation points of Ammen and coastal Laminaria sampled initially in June 1987 and after growth at the transplant sites. With the exception of the

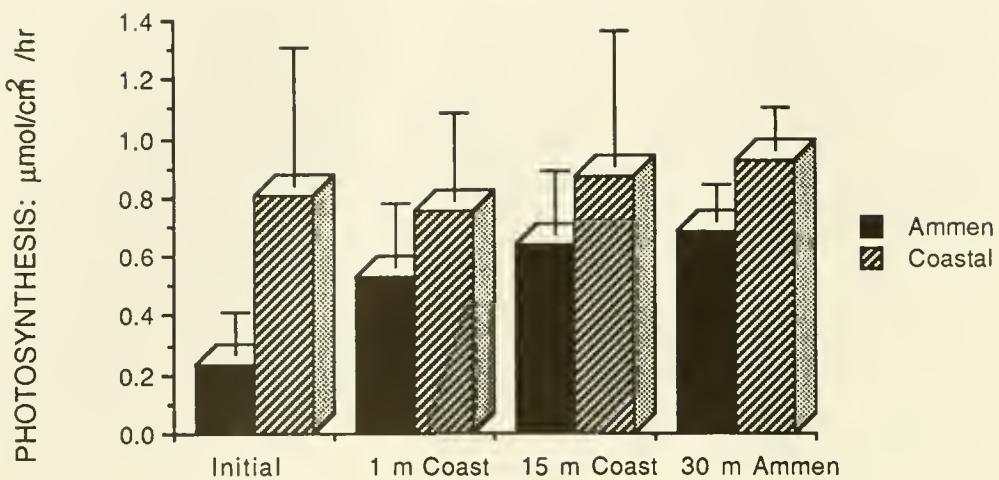


Figure 3. Maximum photosynthetic rates (P_{max}) of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

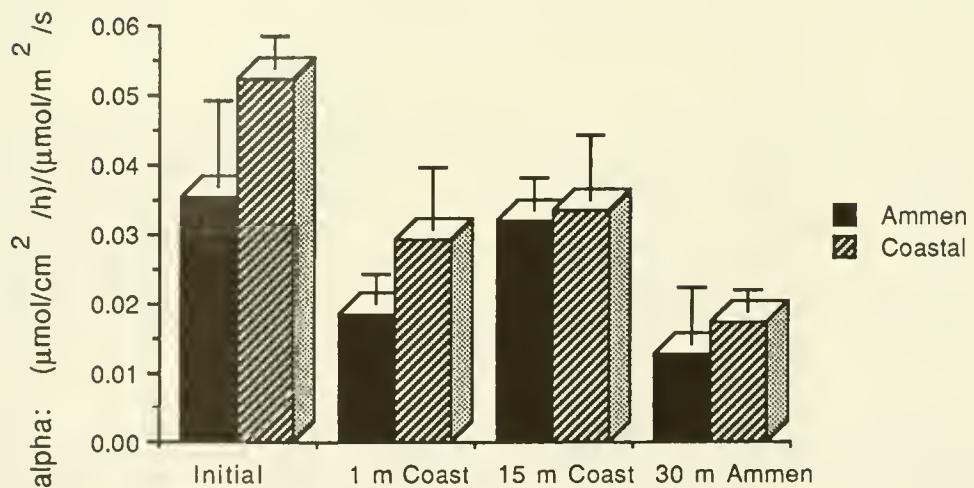


Figure 4. Alpha values of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

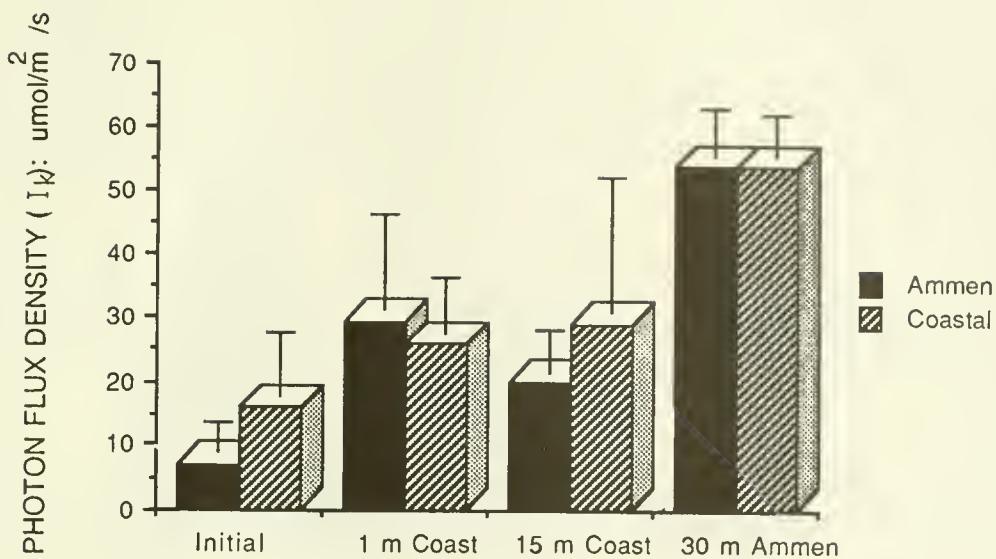


Figure 5. I_k values of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

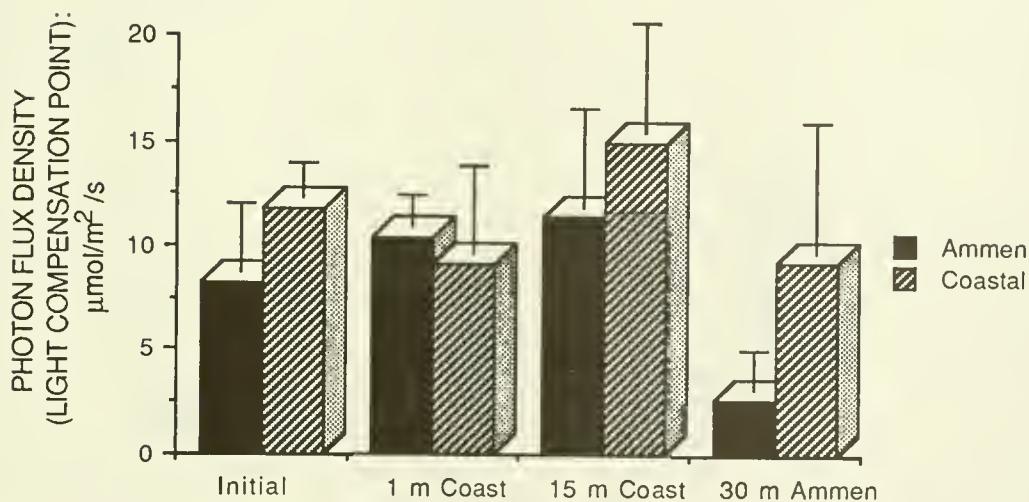


Figure 6. Light compensation points of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

1 m transplant site compensation points were always higher in coastal than Ammen plants, although the difference was only significant at the 30 m site. Significant differences did occur between the two plant groups when data for all of the sites were considered together. The only significant difference within either of the groups of plants with respect to depth was in the Ammen plant at the 30 m site, which had much lower compensation points than those for this group at any other site (2.61 vs 8.26-11.37 umole photons.m⁻².s⁻¹, respectively).

Figure 7 presents data on the rates of respiration of the Ammen and coastal plants. In all cases the respiration rates of coastal plants were higher than those for the Ammen group. However, these differences were only significant for the initial samples and when the data for all sites were pooled.

Figure 8 shows RUBISCO activities of the two groups of plants following initial sampling and after growth at the transplant sites. Significant differences occurred between the two groups of plants both initially and at the 30 m site, with coastal plants having higher values than the Ammen group. RUBISCO activities of the coastal Laminaria were 20.96 and 44.04 nmoles.g f wt⁻¹.min⁻¹ initially and at 30 m, respectively, while those of the Ammen plants were 10.35 and 13.36 nmoles.g f wt⁻¹.min⁻¹ initially and at 30 m, respectively. RUBISCO activities declined in both groups of plants transplanted to the 1 and 15 m coastal sites and did not differ significantly between the two groups being approximately 3.00 nmoles.g f wt⁻¹.min⁻¹ in all cases.

Figures 9, 10, and 11 present data on cellular concentrations of photosynthetic pigments (chlorophyll a, chlorophyll c and fucoxanthin, respectively) in Ammen and coastal Laminaria. With the exception of the 15 m site, coastal plants had significantly more chlorophyll a than the Ammen group (Figure 9). Highest chlorophyll a levels were found in the initial, June 1987, samples (0.353 and 0.661 ug.cm⁻² in Ammen and coastal plants, respectively) and lowest values in the 30 m site (0.137 and 0.321 ug.cm⁻² in Ammen and coastal plants, respectively), with intermediate levels occurring at the 1 and 15 m coastal sites. Chlorophyll c (Figure 10) and fucoxanthin (Figure 11) levels did not differ significantly either between sites or between the two plant groups with the exception of fucoxanthin in coastal Laminaria which were initially higher than those of Ammen plants (0.369 and 0.201 ug.cm⁻², respectively).

Figure 12 shows calculated rates of net carbon fixation in the Ammen and coastal Laminaria populations over a range of daily photon flux densities supplied in a 20:4 L:D photoperiod. Rates were calculated from measured rates of respiration and instantaneous P vs I responses assuming that total daily irradiance was averaged equally over the entire photoperiod. Calculated rates of net carbon fixation were greater in Ammen plants than the coastal population below a photon flux density

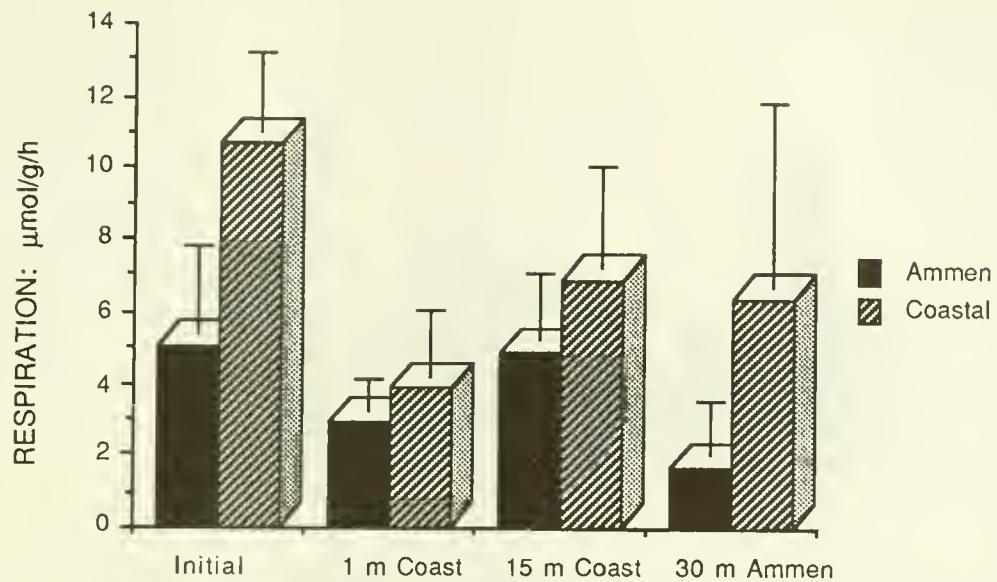


Figure 7. Respiration rates of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

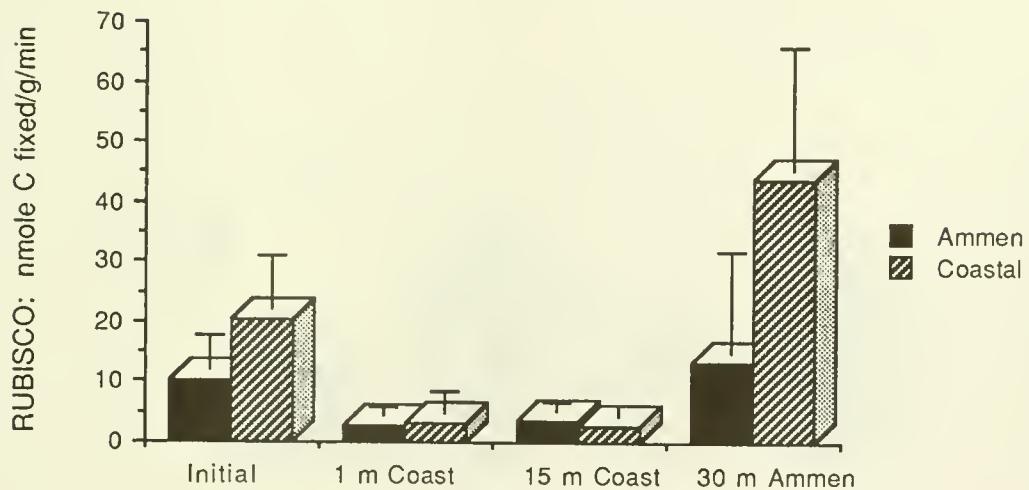


Figure 8. Activities of RUBISCO in initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=3$).

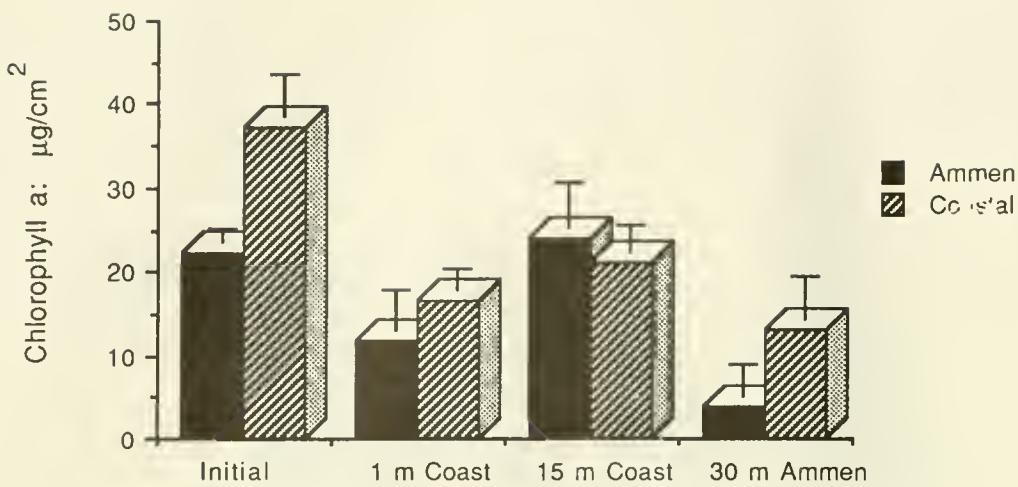


Figure 9. Chlorophyll a content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=3$).

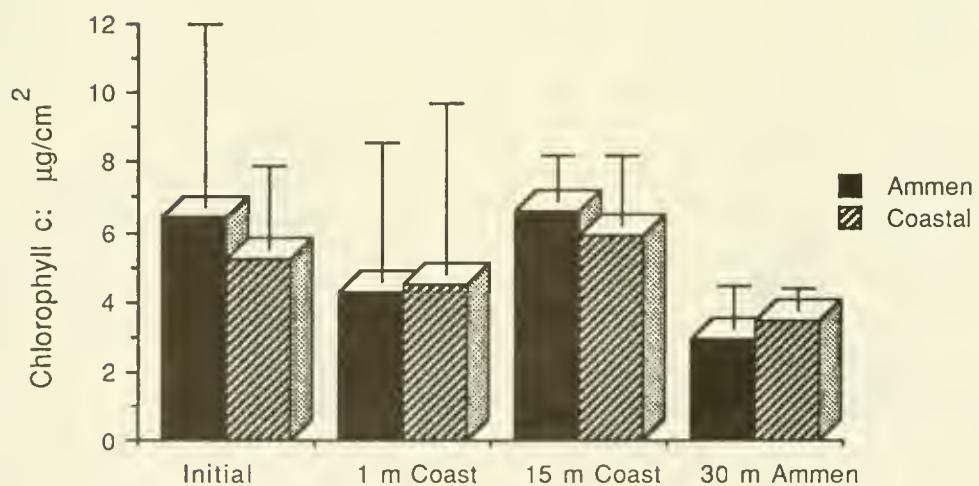


Figure 10. Chlorophyll c content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

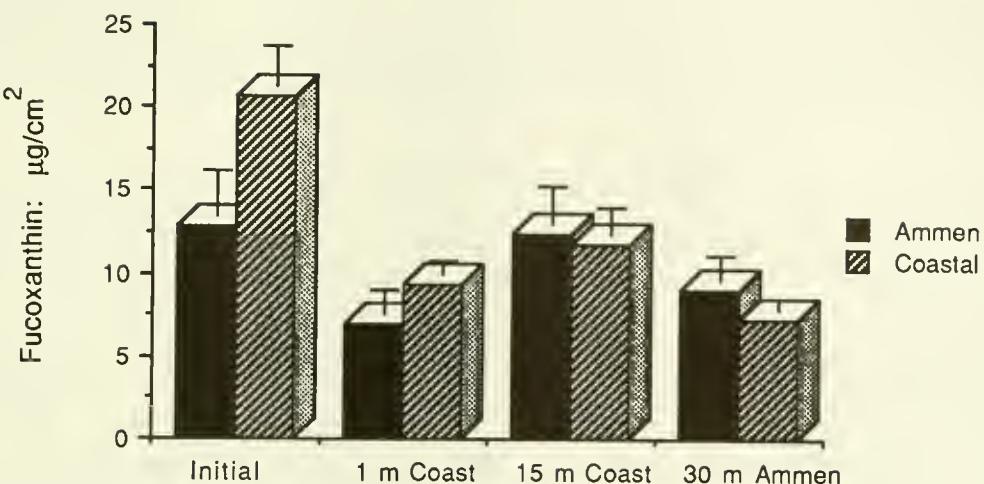


Figure 11. Fucoxanthin content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

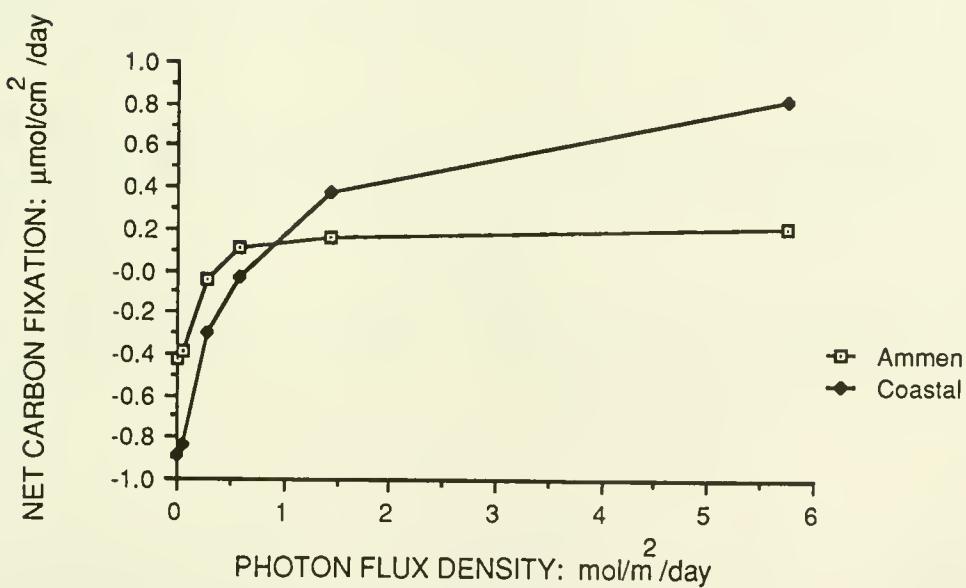


Figure 12. Calculated net daily carbon fixation of Ammen and coastal Laminaria based on data for initial (June) sampling period. This calculation assumes 20:4 L:D photoperiods with different average daily photon flux densities.

of 1.0 umole photons.m⁻².day⁻¹, with Ammen plants achieving net photosynthesis at a photon flux density (0.576 mole photons.m⁻².day⁻¹, 10 umole photons.m⁻².s⁻¹) at which coastal plants experienced a net carbon loss. Above 1 mole photons.m⁻².day⁻¹ the coastal plants achieved higher rates of net carbon assimilation than Ammen Laminaria. Similar patterns were obtained from the P vs I data of the 1, 15, and 30 m transplanted plants (data not shown).

Figures 13, 14, and 15 respectively show the cellular contents of mannitol, amino-N and nitrate in the Ammen and coastal Laminaria initially and following growth at the transplant sites. Initial mannitol levels in the Ammen plants were low (13.58 umole.g f wt⁻¹), whereas those for the coastal Laminaria were high (281.0 umole.g f wt⁻¹). Ammen plants transplanted to the 1 and 15 m coastal sites exhibited considerable increases in cellular mannitol levels to between 350 and 410 umole.g f wt⁻¹, whereas those at the 30 m Ammen site had much smaller increases in mannitol (62.4 umole.g f wt⁻¹). Mannitol levels in the coastal plants remained high at all transplant sites and did not differ significantly from the initial value. Initial amino-N levels were much higher in the coastal than Ammen Laminaria (40.96 cf. 10.92 umole.g f wt⁻¹, respectively) (Figure 14). Amino-N levels were lower in the 1 and 15 m coastal sites and did not differ significantly between the groups. At the 30 m site the Ammen plants had higher levels of amino-N than the coastal group (14.35 cf. 8.61 umole.g f wt⁻¹, respectively). Nitrate contents were undetectable in the coastal Laminaria population at all sites except for the 30 m transplants which had 1.95 umole.g f wt⁻¹. In contrast the initial Ammen plants had an initial cellular nitrate pool of 3.12 umole.g f wt⁻¹ which increased to 59.11 umole.g f wt⁻¹ at the 30 m site but which was lost at the 1 and 15 m coastal transplant sites.

Cellular nitrate reductase activities of the Laminaria plants are shown in Figure 16. Initially, coastal plants had significantly higher activities of this enzyme than Ammen plants (0.348 cf. 0.043 umole.g f wt⁻¹.hr⁻¹, respectively). Activities were similar at the 1 and 30 m transplant sites (0.126-0.156 and 0.025-0.031 umole.g f wt⁻¹.hr⁻¹ at 1 and 30 m, respectively) but were different at the 15 m site where Ammen plants had very low activities (0.007 umole.g f wt⁻¹.hr⁻¹) compared to the coastal group (0.092 umole.g f wt⁻¹.hr⁻¹).

DISCUSSION

The results presented here suggest that genetic differences do exist in the photosynthetic physiology of Ammen and coastal Laminaria plants. Overall, Ammen plants have lower maximum rates of photosynthesis (Fig. 3), lower respiration rates (Fig. 7) and lower light compensation points (Fig. 6) than the coastal L. digitata population. These differences persisted in transplanted plants, grown under similar light conditions, suggesting either

DEEP WATER BENTHIC ALGAL
ZONATION IN THE GULF OF MAINE

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ABSTRACT

Algal community structure is described for a deep-water rock pinnacle in the Gulf of Maine. Three depth zones of algal dominance are apparent and consist of 1) leathery macrophytes (to 40 m), 2) foliose red algae (to 50 m) and 3) crustose algae (fleshy crusts to 55 m and coralline crusts to 63 m). Microscopic filamentous and erect calcareous algae are also present but inconspicuous. Upright macroscopic filamentous and thin sheet-like forms were not observed on the pinnacle. Sea anemones (Metridium senile) dominate some vertical faces and abrupt prominences in the shallowest regions of the pinnacle (to 24 m) and locally appear to set the upper vertical limits of kelp and possibly foliose reds. Laminaria sp. forms an open park-like canopy from 24 to 30 m whereas Agarum cribrosum the deepest kelp, grows as isolated individuals to 40 m. Peyssonnelia sp. and Leptophytum laeve are the deepest occurring fleshy and calcareous crusts, respectively. The occurrence of these algae at record depths for the Gulf of Maine and for cold water marine environments may be the result of an absence of large herbivores and the high productivity potential of the benthos in these relatively clear waters. By compiling data on depth distribution patterns world wide, it is evident that the three zone structure of algal morphologies observed in the Gulf of Maine is a global phenomenon.

INTRODUCTION

Globally, marine plants account for most of the primary production on earth. In many productive coastal regions, a significant portion of the production is from attached macroalgae (Mann, 1973). The vertical limit of this production, however, is restricted to relatively shallow depths which differ from place to place depending on oceanographic conditions. To assess the potential contribution of benthic macroalgae to global marine productivity, we need to know the depth limits or extinction depths (sensu Sears and Cooper, 1978) of these plants. Although research has been conducted on extinction depths of tropical plants, relatively few studies exist for cold water habitats.

In the past decade the use of scuba, manned submersibles,

and remote video devices has extended our knowledge of depth maxima of algal communities significantly (summarized in Table 1). These include discoveries of record extinction depths for the tropical Atlantic (Littler et al., 1985, 1986) and tropical Pacific oceans (Agegian and Abbott, 1985) and the unique deep water kelp communities of the Mediterranean Sea (Mojo and Buto, 1970; Drew et al., 1982). Overall, however, patterns of extinction depth distribution of algae are rare, or spuriously collected, depending on the availability of deep diving submersibles or manned underwater habitats (Earle, 1972; Sears and Cooper, 1978; Littler et al., 1986). Although other deep water collections have been reported, we have not listed them because they represent dredged specimens, (e.g., Laminaria brasiliensis is reported from depths greater than 70 m; Joly and Oliveira Filho, 1967; Oliveira Filho, 1976).

Light is often considered to be the most important element influencing patterns of algal depth distributions. This was recently reviewed by Hiscock (1986, p. 294) who stated:

"Several studies, including those published by Boulter et al. (1974), Norton et al. (1977) and Luning and Dring (1979), have indicated that the critical depth below which kelp fail to grow is where about 1% of surface illumination is reached. For the foliose red algae, the critical depth is that at which c. 0.1% of surface illumination penetrates."

Hiscock's (1986) review indicated that algal extinction depths are constant for kelp and foliose algae when considered as a function of the percentage of surface irradiance. This suggestion has not been tested in the western North Atlantic which contains a different subtidal algal flora.

What little is known of algal depth patterns in the western North Atlantic Ocean has been described largely from nearshore scuba observations (Lamb and Zimmerman, 1964; Edelstein et al., 1969; Adey, 1973; Sears and Wilce, 1975; Steneck, 1978; Mathieson, 1979; Himmelman, 1980; Mathieson et al., 1981). Relatively few direct observations have been made subtidally on offshore islands or submerged ledges (but see Sears and Cooper, 1978). These offshore habitats are important to study, however, because their geographic isolation and oceanic character make them unique. Additionally they may provide insight into processes such as recruitment, productivity, herbivory and evolutionary relationships which are important to more broadly distributed nearshore communities.

Here we describe the algal assemblage of a submerged pinnacle that lies well offshore in the Gulf of Maine and has a relatively shallow (24m) summit. We report several new depth records for the North Atlantic, the existence of a deep water Laminaria "park" (sensu Kitching, 1941) and a three zone depth pattern of algal dominance which we believe may be a worldwide

TABLE 1
Summary of benthic algal depth maxima for various biogeographic provinces.

CITATION	LOCATION	BIOGEOGRAPHIC PROVINCE	ALGAL SPECIES OR FORM	DEPTH (M)
Lang 1974	Jamaica	TROPICS	Crustose red and filamentous green	175
James & Ginsburg 1979	Glovers reef		Crustose coralline	250
		SUBTROPICS	" <i>Lithothamnia</i> "	175
Littler et al. 1985	Bahamas		Crustose coralline	268
Littler et al. 1985	San Salvador		<i>Ostreobium</i>	210
Littler et al. 1985	San Salvador		<i>Peysonnelia</i>	189
Littler et al. 1985	San Salvador		Johnson-Sea-Linkie profunda	157
Littler et al. 1985	San Salvador		<i>Halimeda copiosa</i>	130
Littler et al. 1985	San Salvador		<i>Lobophora variegata</i>	88
Littler et al. 1985	San Salvador		Foliose seaweeds	100
Taylor 1928	Florida		Foliose algae	200
Doty et al. 1974	Hawaii		Crustose coralline	366
David et al. 1904			<i>Syringoderma</i>	90
Henry 1984	Florida	Subtropical N. Atlantic		
		MEDITERRANEAN	" <i>Lithothamnia</i> "	120
Molnier 1960ab	Corsica		Varied	75
Drew 1969	Maltese archipelago		<i>Laminaria</i>	95
Mojo & Buta 1971	Straits of Messina		<i>Laminaria</i> and others	25
Giaccone, 1972	Straits of Messina		<i>Laminaria rodriguezii</i>	95
Fredj 1972	Corsica		" <i>Lithothamnia</i> "	120
Fredj 1972	Corsica		<i>Laminaria</i>	55
Drew 1974	Straits of Messina		<i>Laminaria</i>	55
Drew et al. 1982	Straits of Messina			
		BOREAL-TEMPERATE		
Boutler et al. 1974	Roscoff	Temperate E. Atlantic	<i>Laminaria hyperborea</i>	25
Ernst 1966	Bretagne		<i>Laminaria hyperborea</i>	30
Kain 1971	Isle of Man		<i>Laminaria hyperborea</i>	20
Castric-Fey et al. 1973	de Glenan Archipelago		<i>Laminaria hyperborea</i>	30
Castric-Fey et al. 1973	de Glenan Archipelago		Various algae	47
Kain 1976	British Isles		<i>Laminaria hyperborea</i>	24
Kain 1971	Isle of Man		<i>Laminaria hyperborea</i>	19
Luning & Dring 1979	Helgoland		<i>Laminaria hyperborea</i>	8

Maggs & Guiry 1982	Ireland	Boreal E.	Atlantic	<i>Laminaria hyperborea</i>	32
Cullinane & Whelan 1983	Ireland	Boreal E.	Atlantic	<i>Laminaria hyperborea</i>	22
Cullinane & Whelan 1983	Ireland	Boreal E.	Atlantic	<i>Delesseria sanguinea</i>	27
Jorde 1966	Bergen Norway	Boreal E.	Atlantic	<i>Laminaria hyperborea</i>	30
Lamb & Zimmermann 1964	Cape Ann, MA	Subarctic W.	Atlantic	<i>Laminaria</i>	12
Lamb & Zimmermann 1964	Cape Ann, MA	Subarctic W.	Atlantic	<i>Foliose Reds</i>	20
Sears & Cooper 1978	Gulf of Maine	Subarctic W.	Atlantic	<i>Foliose Red Algae</i>	38
Sears & Cooper 1978	Gulf of Maine	Subarctic W.	Atlantic	<i>Crustose Corallines</i>	47
Mathieson 1979	Gulf of Maine	Subarctic W.	Atlantic	<i>Crustose Corallines</i>	24
Mathieson et al. 1981	Gulf of Maine	Subarctic W.	Atlantic	<i>Laminaria</i> spp.	24
Mathieson 1979	Gulf of Maine	Subarctic W.	Atlantic	<i>Crustose and filamentous *algae</i>	18
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>L. longicruris</i>	32
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>L. solidunguilla</i>	30
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Lithothamnion tophiforme</i>	40
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Phymatolithon laevigatum</i>	40
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Phyllophora</i>	37
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Agarum cribosum</i>	25
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Turnerella perryi</i>	25
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Lithothamnion galactiale</i>	30
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Ptilota serrata</i>	30
South 1983	Newfoundland	Subarctic W.	Atlantic	<i>Peysonnelia</i>	30
Sears in Press	Georges Bank	Subarctic W.	Atlantic	<i>Foliose Red Algae</i>	48
Sears in Press	Georges Bank	Subarctic W.	Atlantic	<i>Crustose Coralline</i>	53
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Laminaria longicruris</i>	30
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Laminaria</i> sp.	35
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Agarum cribosum</i>	40
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Foliose reds</i>	50
This Study	Gulf of Maine	Subarctic W.	Atlantic	<i>Algal crusts</i>	63

phenomenon. An interesting and important feature of the Ammen Rock site is the lack of large herbivores, especially sea urchins, which may contribute to the establishment and persistence of these macroalgal assemblages at record depths.

MATERIALS AND METHODS

During the summers of 1984 and 1985 we made a series of dives with the 2-man submersible, Mermaid II, 4-man submersible Johnson Sea-Link and an unmanned reconnaissance vehicle, Recon IV, as a part of NOAA's National Undersea Research Program. We report here on the results of two Recon IV surveys and four Mermaid II and Johnson Sea-Link dives on a shallow pinnacle (ca 24 m) near Ammen Rock which is part of Cashes Ledge approximately 104 km east of Boothbay Harbor, Maine (Fig. 1).

Our study site, called "Ammen Rock Pinnacle" is located in the center of the Gulf of Maine and is influenced by strong currents and oceanic water masses of low turbidity (we observed up to 30 m lateral visibility, see also light data below) and high salinity. Water temperatures from June to August are typical for Maine Intermediate Water (Hopkins and Garfield, 1979) and ranged from 5°C to 9°C at the summit of the pinnacle and from 5°C to 6.5°C at 75 m. Typically however, benthic temperatures ranged from 5.5°C to 7.5°C in the photic zone. The Ammen Rock Pinnacle consists of a steeply sloping granitic outcrop. The walls descend sharply from the summit to about 30 m and then at a lesser angle to 43 m. Large boulders lie at the base of the pinnacle forming a talus slope. Below 43 m, boulders and ledge outcrops form most of the available hard substrata, gradually being replaced by cobbles rocks, sand and small outcrops of ledge. Sediment accumulations increase with depth and increasingly reduce the amount of primary substratum on horizontal surfaces below 50 m.

Visual (recorded with cassette tape), photographic and video observations were made on the submersible dives. The submersibles were equipped for limited collecting with a suction sampler and a manipulator arm. Neither collection technique was satisfactory but between them provided voucher specimens or fragments of several algae. Rocks encrusted with coralline algae up to 30 x 30 cm in size were collected with the manipulator arm. During 1985 limited scuba diving was permitted to 30 m to collect algae. Underwater light readings were made in 1985 by Dr. James Sears with a Licor Underwater Photometer Model Li 185B with a cosine corrected sensor. The unit measures PAR in the 400-700 nm waveband and the unit of measurement is u. A series of 5 tests were run over a two day period at midday during calm clear weather conditions. For comparison a similar test was run with a Licor Model 188b integrating quantum meter with a Li 905B spherical sensor during calm conditions on the coast at Pemaquid, Maine.

Data records of algal observations were pooled from our

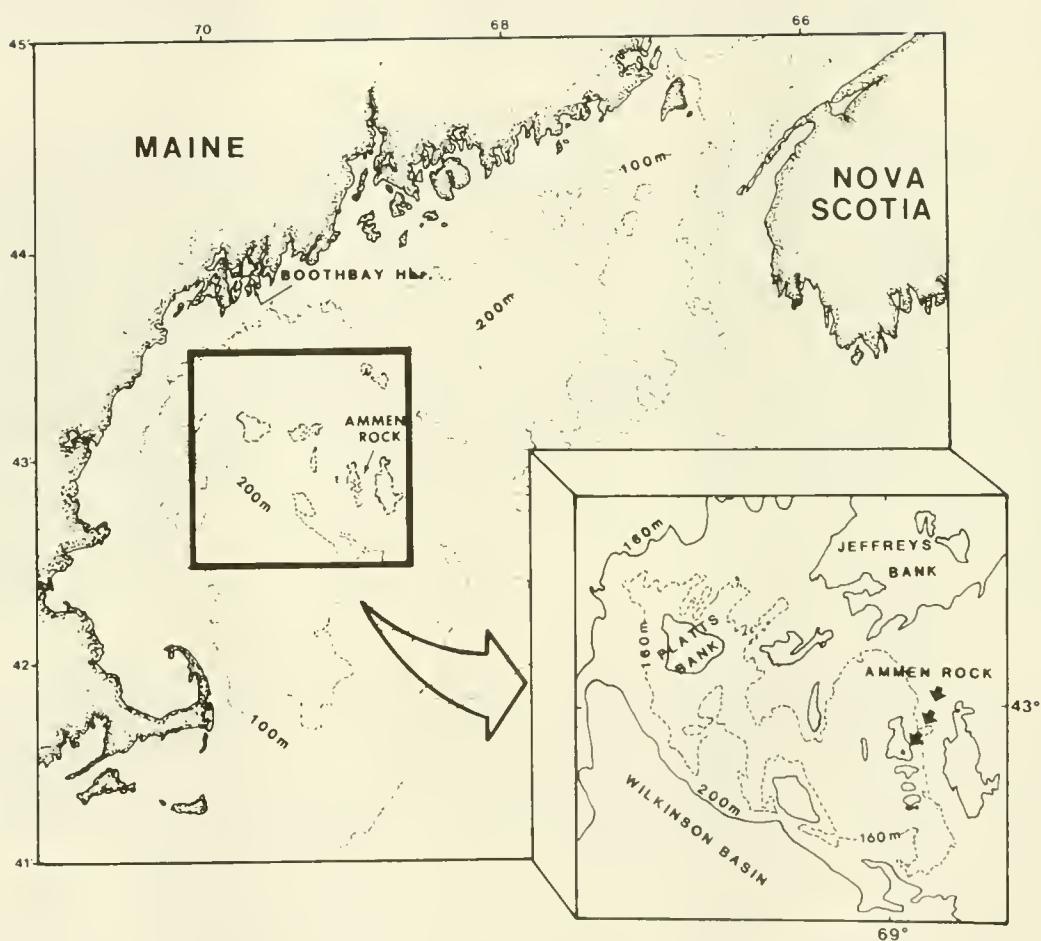


Figure 1. Location of study site at Ammen Rock Pinnacle in the Gulf of Maine.

observations and those made by J. Sears, K. Sebens and J. Witman.

RESULTS

Seventeen algal species were recorded from Ammen Rock Pinnacle including three kelps, five foliose reds, two small filamentous forms, three fleshy red crusts, three crustose corallines and one erect articulated calcareous alga (Table 2). Surprisingly, large filamentous and thin sheet-like algae were not observed on the pinnacle. All of the specimens observed or collected at these depths appeared healthy and several were reproductive. Interestingly, the thallus sizes of kelps were sharply truncated at the deepest depths. Typically the maximum size of thalli for each taxon decreases with depth. Kelps, for example, ranged in size from 100-200 cm near the summit to 10-20 cm at the lowermost limits.

A striking zonation pattern exists on the pinnacle (Fig. 2). The summit of one of the shallower peaks (observed in 1984 but not located in 1985) was not examined in detail but the upper walls (ca 23m) were covered by dense carpets of sea anemones, Metridium senile. Kelps began at 24m and co-occurred with sea anemones over much of their range to a depth of 40m. Foliose red algae grew in the kelp zone and extended to a depth of 50m. Corallina officinalis was observed at 24 to 30m whereas calcified (coralline) and non-calcified (fleshy) algal crusts were observed at all zones having algae. Peyssonnelia was the deepest occurring fleshy crust (55 m) whereas Leptophytum laeve was the deepest coralline crust and alga observed on the pinnacle (63m).

Invertebrate populations were also zoned with depth. Below the shallow band of M. senile from 50-90m were patchy assemblages of sponges (Haliclona, Suberitechinus, Polymastia, and Phakellia), ascidians (Aplidium, Ascidia, and Botryrilloites), and two other anemones (Tealia and Bolocera). Also invertebrates such as Modiolus and Myxicola were abundant in places at this depth range. Most conspicuous in their absence within the zones of algae were sea urchins. All other herbivores were rare. We collected a few small limpets and chitons but these would have little impact on benthic algae.

The kelp zone was occasionally sandwiched in places between dense beds of Metridium. The dominant kelp was a Laminaria species of uncertain taxonomic affinity but which resembles L. digitata. The great depths to which this species grows, aspects of its morphology (described below) and anatomy (presence of mucilage ducts in the frond and stipe) suggest that this may be a new taxon. This Laminaria formed an open or park-like canopy (sensu Kitching, 1941; Luning and Dring, 1979) mainly between 25-30m. Individual stipes were spaced 0.2 to 0.5 m apart. Fronds of this species were up to 2m in length with wide, sparsely digitate lamina with one or two conspicuous vertical constrictions. The latter apparently occur annually suggesting that the larger fronds survive for a

TABLE 2

DEPTH RANGES AND REPRODUCTIVE PATTERNS OF
ALGAE AT AMMEN ROCK PINNACLE

<u>Species</u>	Depth Range & Maxima ¹	Reproductive Condition ²
LEATHERY MACROPHYTE ASSEMBLAGE (To 40 M)		
<u>Agarum cibrosum</u> (Mertens) Bory	24-33*-40 M	MS
<u>Laminaria longicruris</u> De la Pylaie	24-30*	NR
<u>Laminaria</u> sp. Lamouroux	24-27*-35	NR
FILAMENTOUS ASSEMBLAGE (To 33 M)		
<u>Audouinella purpurea</u> (Lightfoot) Woelkerling	24-33*	NR
<u>Uronema curvata</u> Printz	24-33*	NR
FOLIOSE ASSEMBLAGE (To 50 M)		
<u>Callophyllis cristata</u> (C. Agardh) Kutz	24-33*-40	CS
<u>Membranoptera alata</u> (Hudson) Stackhouse	24-33*-40	CS
<u>Phyllophora truncata</u> (Pallas) A. Zinova	40	
<u>Phycodrys rubens</u> (Linnaeus) Batters	24-33*-50	NR
<u>Ptilota serrata</u> Kutz	24-33*-50	CS
ARTICULATED CALCIFIED ASSEMBLAGE (To 33 M)		
<u>Corallina officinalis</u> Linnaeus	24-33*	C
CRUSTOSE ASSEMBLAGE		
Non-calcified forms (To 55 M)		
<u>Petrocelis</u> sp. ³	30-43*	NR
<u>Peyssonnelia</u> sp. ⁴ Decaisne	30-55*	NR
<u>Cruoriopsis</u> sp.	43*	NR
Calcified forms (To 63 M)		
<u>Leptophytum laeve</u> (Stroemfelt) Adey	24-61*-63	TS (61M)
<u>Lithophyllum orbiculatum</u> (Foslie) Foslie	24-43*	TS (30M)
		43
<u>Lithothamnium lemoineae</u> Adey	24-49*	NR

1) *Indicates species identified from collected specimens. Depth ranges of species without an asterisk were determined visually or from video.

2) NR=Not reproductive, MS=Meiosporic, CS=Cystocarpic, TS=Tetrasporic.

3) This may be the alternate stage for Gigartina.4) This may be the alternate stage for Gloiosiphonia.

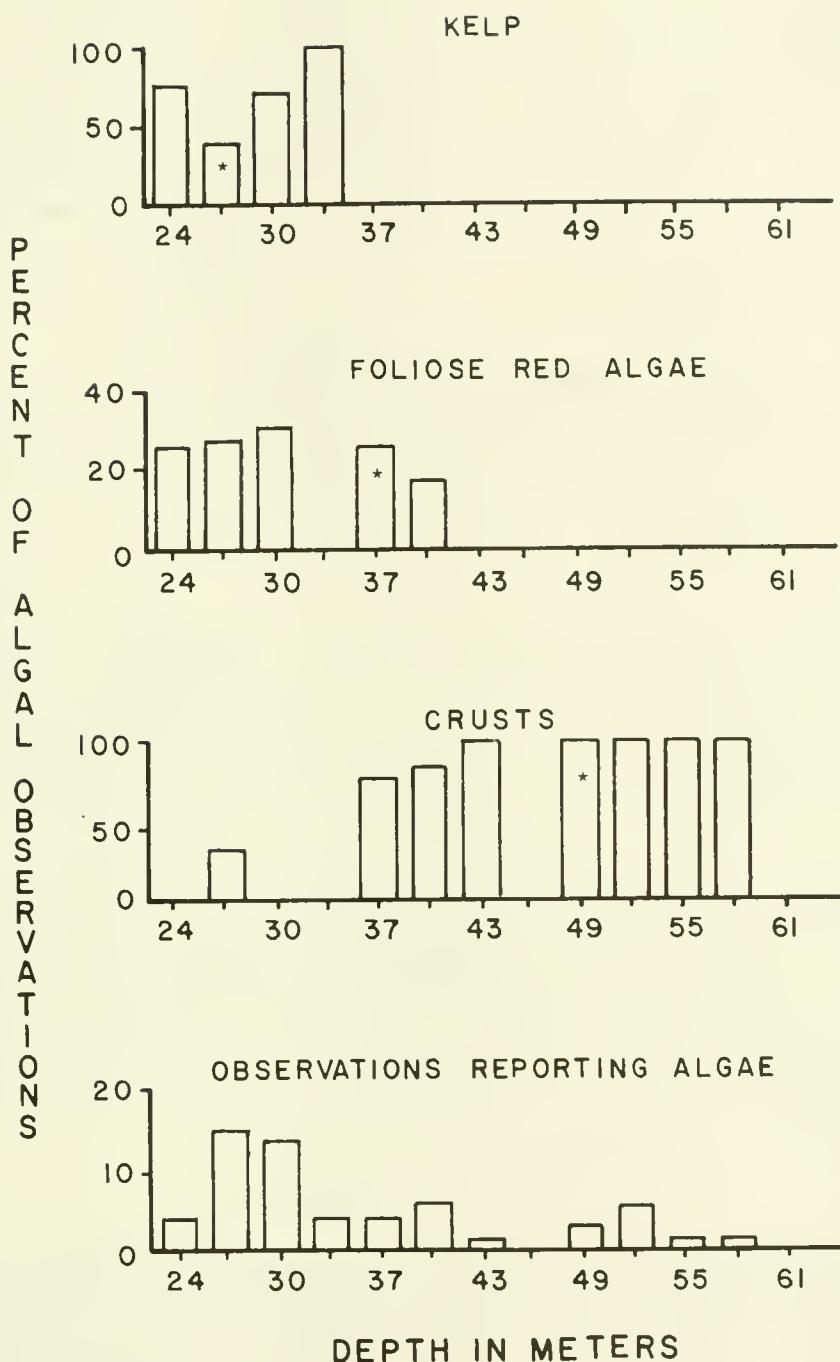


Figure 2. Relative abundances of major algal assemblages at Ammen Rock Pinnacle as a function of depth (species listed in Table 1). Abundances were determined by counting the frequency of all observations during 1984 (Recon IV and Mermaid II study). Asterisk indicates a depth where an algal assemblage was reported to be dominant (> 50% cover).

period of 2 to 3 years. The structure of the holdfast also appears to support this interpretation, which usually shows two to three (occasionally seven) distinct whorls of haptera. Locally, we observed a striking pattern of broad clear areas surrounding many of the Laminaria plants. These halos presumably were due to whiplash effects from the long sweeping fronds. Agarum cibrosum was the deepest recorded kelp (40m), although small non-digitate plants resembling the genus Laminaria were also observed in the same zone (35-40m) but could not be collected. Laminaria longicruris was extremely rare and interspersed with Laminaria sp. at the shallower depths.

Foliose red algae were dispersed among kelp and on ridges between dense stands of anemones where they formed narrow dense patches. They also occurred singly or as tiny, inconspicuous tufts. Dominant in this assemblage was Ptilota serrata and Phycodrys rubens (about equally abundant). We also found Callophyllis cristata, Membranoptera alata and Phyllophora truncata (Table 2).

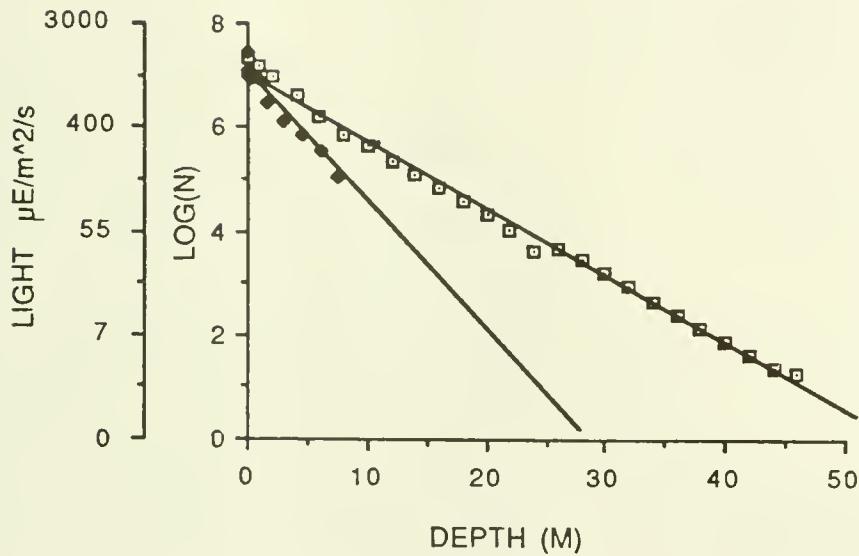
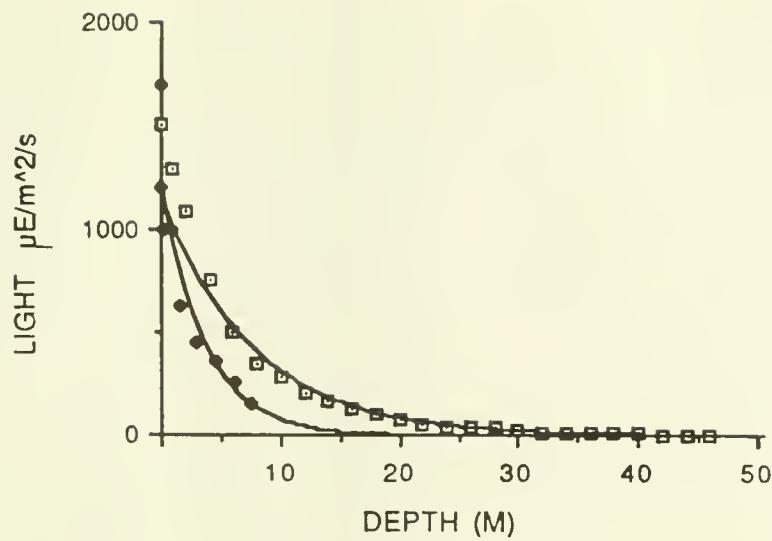
Both calcified and noncalcified crusts were found in all zones. Fleshy crusts are found slightly shallower (to 55m) than are coralline crusts (to 63 m) (Table 2). Coralline abundance was considerable at depths over 50 meters and was observed to cover up to 80% of the rock substrate in places. The dominant fleshy crust was Peyssonnelia and the dominant coralline crusts were Lithophyllum orbiculatum at 30 m and Leptophyllum laeve at 55-63 m.

Underwater light readings revealed marked differences between Ammen Rock Pinnacle and the coast of Maine due to the turbidity of the water (Fig. 3). Both profiles approximate a linear function when natural log-transformed and show that light penetration at Ammen Rock is significantly greater. When expressed as percent of surface irradiance the light levels corresponding to the extinction depths of the three major functional-form groups are: 0.44% for kelps, 0.11% for foliose red algae and 0.02% for coralline crusts.

DISCUSSION

We found three distinct algal assemblages zoned with depth at the Ammen Rock Pinnacle. This pattern is not unlike those found in shallower nearshore regions throughout the Gulf of Maine and elsewhere. The patterns are recognizable as assemblages of morphologically similar species which represent distinct functional groups (sensu Littler and Littler, 1980; Steneck and Watling, 1982). Three of these groups; leathery macrophytes, foliose algae and crustose algae dominate the three depth zones respectively (Fig. 2).

The maximum depth for each of the three algal zones exceeds that known for the Gulf of Maine and for any boreal-subarctic environment (Table 1 and Fig. 4). This is probably due to the



◻ Ammen Rock Pinnacle 4 July 1985

◆ Pemaquid Point, Me. 25 July 1980

Figure 3. Light attenuation in coastal (Pemaquid Point, Me.) and offshore (Ammen Rock Pinnacle) habitats. Upper graphs are untransformed data with regressions of $y = 1218 \times 10^{(-0.12x)}$, $R = 0.98$ for Ammen Rock Pinnacle and $y = 1148 \times 10^{(-0.06x)}$, $R = 1.00$ for Pemaquid Point, Me. Lower graphs are natural log transformed data with regressions of $y = 7.0 - 0.13x$, $R = 1.00$ for Ammen Rock Pinnacle and $y = 7.1 - 0.27x$, $R = 0.98$ for Pemaquid Point, Me.

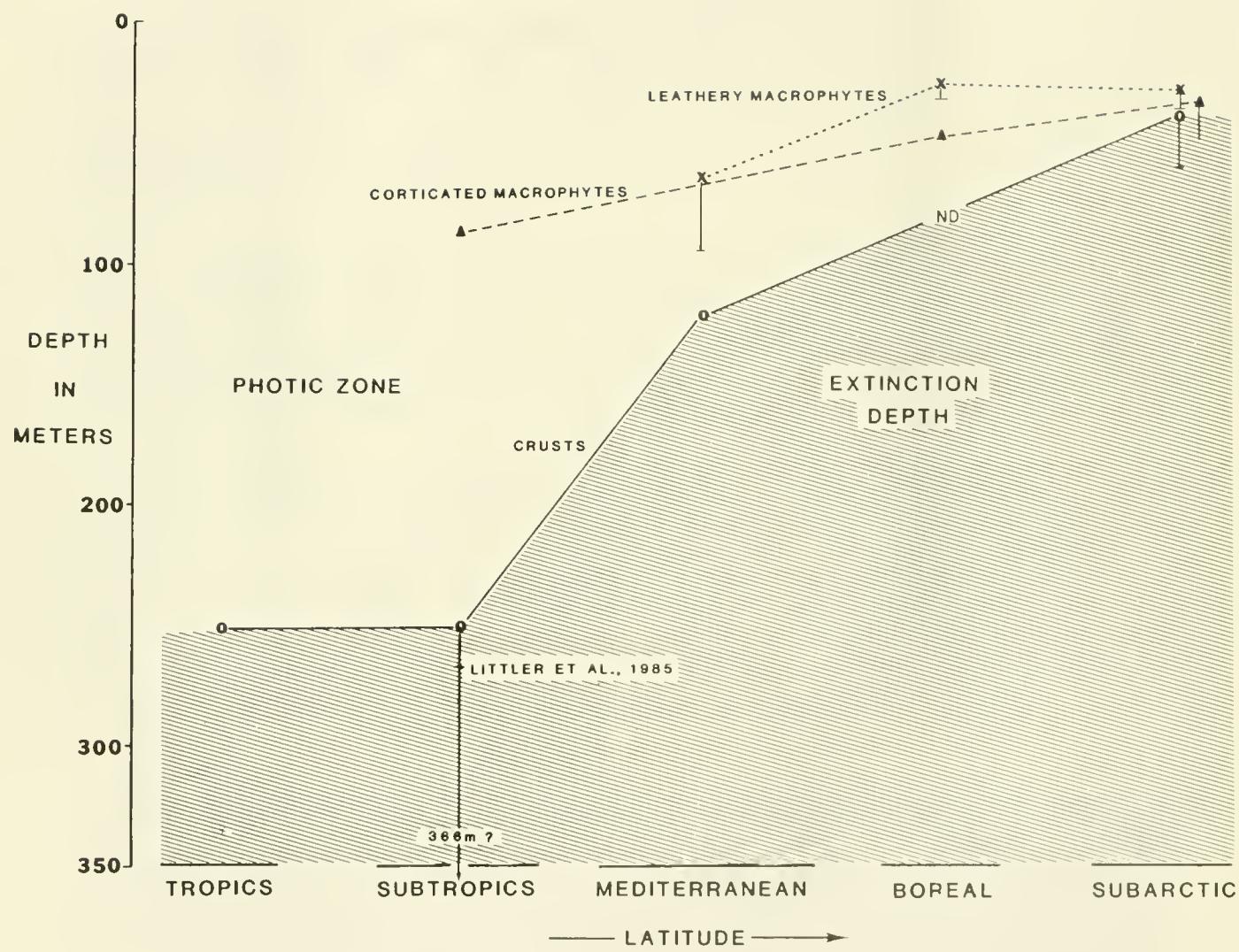


Figure 4. Biogeographical depth patterns for these algal functional groups (based on literature cited in Table 1 and this study).

clarity of water and absence of herbivores at Ammen Rock Pinnacle. Both factors are important but light levels undoubtedly are more important at this site. Although extinction depths vary greatly depending on water clarity, traditionally the percent of surface illumination correlating with algal depth limits is thought to remain rather constant (Hiscock, 1986). Our data conforms with other published studies for algal crusts (.02% of surface illumination, Sears, 1987 but see Luning and Dring, 1979; Hiscock, 1986), and foliose algae (.1% of surface illumination, Luning and Dring, 1979; Hiscock, 1986; Sears 1987). However, we found kelp growing at significantly lower light levels (0.44%) than previously reported (0.7% Luning and Dring, 1979 and Sears, 1987; 1% Hiscock, 1986). Littler et al. (1985), however, observed lower light intensities for tropical algae (.05% foliose algae, .0005% crustose corallines). Thus percent surface illumination may provide a good rule of thumb for certain regions and forms but the values are not absolute.

Although the depth maxima of algae are set by light, the virtual absence of herbivores from the pinnacle is significant. Sea urchins are dominant structuring forces in much of the Northwest Atlantic (Breen and Mann, 1976) and Gulf of Maine (Sebens, 1985; Witman, 1985; Vadas et al., 1986). The causes for their absence from the pinnacle is unknown, although preliminary experiments suggest predation from fishes is involved (Steneck and Vadas, unpublished data). Nonetheless it is the absence of herbivores that allows the presumed physiological depth limits of these fleshy algae to be expressed.

Another unusual feature is the local dominance of anemone patches (*M. senile*) on vertical rock walls and prominences near the summit of the pinnacle. In part this may be due to the formation of dense mats (possibly clones) on most shallow outcrops. Clonal development in marine organisms is an effective strategy for occupying primary space in the subtidal zone (Jackson 1979) and thus competition may be preventing locally the extension of kelps and other algal groups into these patches.

There is a clear pattern in the zonation of algal species and functional groups on the pinnacle. Both species and functional group diversity is greatest at the shallowest depths. The successive loss with depth of leathery macrophytes, corticated macrophytes, noncalcified crusts and finally calcified crusts seen at Ammen Rock Pinnacle (Fig. 2, Table 2) is also a global phenomenon (Table 1, Fig. 4). Although it has long been recognized that shallow zones dominated by large leathery macrophytes also have a diverse understory of species and other functional groups such as, corticated macrophytes, foliose, filamentous and crustose forms (Dawson et al., 1960, Neushul, 1967), the universality of this subtidal zonation pattern at a functional group level has gone unrecognized. Lamb and Zimmerman (1964) and Neushul (1967) recognized a tripartite pattern of zonation but these zones were identified by the dominant species not morphologies. For example, they identified

shallow Laminaria zone, a deeper Agarum zone and a diverse assemblage of two or three functional groups in the deepest zone. Other studies on subtidal zonation have correlated differences in pigment composition ("chromatic adaptation") with depth such that from shallow to deep water: brown, green and red algae (Larkum et al., 1967; Dring, 1981; Littler et al., 1986) are said to dominate respectively. Interestingly at Ammen Rock Pinnacle, there is no green zone, the brown zone is compressed and the red zone exists over the entire vertical range of algae. Although our site may be too deep for a green zone, the zonation pattern appears to correspond more closely to morphological types than to pigmentation.

The repeating pattern of zonation at a functional group level begs the question: are these morphologies adaptive, and if they are what is it about them that allow certain forms to consistently dominate particular depth zones? Littler et al., (1986) have, in part, provided an answer, by showing that encrusting tropical deep water algae are photosynthetically two to three orders of magnitude more efficient than algae exposed to near surface light environments. This paper provides a first step in documenting the patterns in distribution and abundance for a temperate/boreal community - the processes controlling those patterns will require further study.

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COMPARATIVE PHOTOSYNTHETIC PHYSIOLOGY OF SHALLOW AND DEEP WATER
POPULATIONS OF LAMINARIA IN THE GULF OF MAINE

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INTRODUCTION

Previous research indicated the occurrence of a deep water population of Laminaria at Ammen rock and Ammen rock pinnacle in the central Gulf of Maine (Vadas and Steneck, 1988). The Ammen Laminaria closely resembles Laminaria digitata, which occurs through the North Atlantic including the coast of Maine. Ammen plants differ from coastal L. digitata by having narrower and less digitate blades, by possessing mucilage ducts in the stipe and holdfast and by the frequent occurrence of whorls of haptera in the holdfast. Furthermore, the Ammen Laminaria population occurs at considerable depth (25-35 m), whereas L. digitata typically has maximum abundance in shallow water. By themselves these differences are not sufficient to justify placing the Ammen Laminaria in a separate taxon from L. digitata. L. digitata is known to exhibit considerable phenotypic plasticity (Sundene, 1964) and the taxonomic significance of mucilage ducts is open to question (Chapman, 1973). However, recent preliminary studies indicate that large differences occur between chloroplast DNA sequences in Ammen Laminaria and coastal L. digitata (Fain, Vadas and Steneck, unpublished), suggesting that Ammen Laminaria may be a distinct species.

Thus, it is currently an open question as to whether or not the Ammen Laminaria is a new species, or if it is a deep water ecotype of L. digitata. Irrespective of the taxon to which the Ammen Laminaria population is eventually assigned, a key question is what, if any, adaptations have evolved for life in a deep water environment characterized by low light levels. *A priori* one would expect this population to have evolved adaptations to low irradiance because of the small size and extreme isolation of the population (Vadas and Steneck, 1988), which is continuously exposed to low light levels. In contrast, most coastal Laminaria populations are contiguous from shallow to deep water and hence experience a gradient of irradiance.

The objectives of the present study were to determine if the Ammen Laminaria population does possess specific adaptation to low light levels and to determine their nature. The experimental design involved a comparative study of the Ammen population with a

shallow water population of L. digitata. Because the physiological characteristics of the two populations will reflect both genetic differences and phenotypic acclimation to the light levels at the two sites, reciprocal transplants were performed in order that comparisons could be made between sporophytes from the two populations which had been exposed to similar irradiance levels. These experiments were performed during the summer 1987 cruises of the RV Powell and RV Seward Johnson in the Gulf of Maine.

METHODS

Two populations were studied: a shallow water Laminaria digitata (Huds.) Lamour. population growing 1 m below mean low water at Thread-of-Life in Maine, and the Ammen population described previously (Vadas and Steneck, 1988) growing at 30 m at Ammen rock pinnacle. Initial samples were taken from these sites in late June 1987. 10 plants from each group were transplanted to each of three transplant sites: 1 m and 15 m at Pemaquid (a coastal site close to Thread-of-Life) and 30 m at Ammen rock pinnacle. Transplants had a blade length of between 30 and 60 cm. Plants were transplanted by opening the weave of short lengths of polypropylene rope to admit the holdfast and stipe of tagged plants. The polypropylene ropes were then attached to an anchored buoyed nylon line. Transplants at the coastal site were retrieved in late August 1987, immediately prior to the second cruise to Ammen rock. The 30 m Ammen transplants were retrieved in early September 1987. Plants were collected, and transplant manipulations performed, by SCUBA divers. Plants were transported between the two coastal and Ammen sites and to the laboratory at the University of Maine (Orono campus) in cold (5°C) seawater in large insulated coolers.

Growth of the transplanted Laminaria was monitored by the hole punch technique of Parke (1948). Five sporophytes were collected from each field site in June and taken to Orono for measurements of initial photosynthetic characteristics, activities of enzymes of carbon and nitrogen metabolism and biochemical analysis. Similar measurements were made on subsamples (n=5) of both plant groups after growth at the transplant sites. In the case of plants from the 1 and 15 m coastal sites these measurements were made at Orono, with the measurements on the 30 m Ammen transplants being made onboard the RV Seward Johnson.

Photosynthetic and respiratory measurements were made on 1.95 cm diameter discs punched from the blade 15-25 cm above the stipe-blade transition. Discs were held overnight (18 hr) in aerated seawater at 5°C and a photon flux density of 50 umole photons.m⁻².s⁻¹ in a 16:8 L:D photoperiod. This procedure allows wound healing to occur (Bidwell and McLachlan, 1985). Discs of L. digitata and Ammen Laminaria plants both release copious quantities of mucilage immediately after being cut. Discs were placed in the reaction chamber of a calibrated Rank oxygen

electrode together with 5 ml of millipore filtered (0.45 μ m pore size) seawater. Temperature was maintained at 15°C by a refrigerated thermostatic circulator connected to the water jacket of the electrode chamber. The output of the oxygen electrode was recorded on a strip chart recorder. The sensitivity of the measurements was increased by setting the chart recorder at 1 mV rather than 10 mV (the full scale output of the Rank electrode), offsetting the zero with a Baily RC-10 recorder calibrator.

The oxygen content of the filtered seawater was adjusted to 50-60% of saturation by sparging with nitrogen. Respiration rates were measured by enclosing the reaction chamber in a double layer of thick black cloth. Once a stable respiration rate was achieved the disc was illuminated with successively higher photon flux densities from 1.0 to 600 umole photons. \cdot m $^{-2}$.s $^{-1}$ supplied by a slide projector. Photon flux densities were varied by means of Schott glass neutral density filters. Light levels were increased once a stable rate of oxygen flux was achieved at the previous photon flux density. The entire process took approximately 45-60 min. There was no evidence of photorespiration or nutrient limitation. Measurements were corrected for oxygen consumption by the electrode. Determinations were made on a single disc from each of 5 replicate plants.

Activities of the key Calvin cycle enzyme ribulose-1,5-bisphosphate carboxylase oxygenase (RUBISCO) and the key nitrogen assimilatory enzyme nitrate reductase (NR) were measured as described previously (Davison and Davison, 1987; Davison, 1987). Pigments were analyzed on discs used for photosynthesis measurements by extraction in DMSO and methanol as described by Seely et al. (1972). A further series of discs were extracted with hot 90% ethanol for the determination of mannitol, amino-N and NO_3^- as described previously (Davison and Davison, 1987).

Statistical analysis was performed on the data using 1 or 2 way ANOVA. Non-normal data was analyzed by ANOVA on data ranked using the Kruskal-Wallis procedure. Comparison of means was based on the Student Newman Keuls test. All statistical procedures were done using SAS version 5.16.

RESULTS

Growth rates of transplanted Ammen and coastal Laminaria are shown in Figure 1. Ammen plants transplanted to the 1 m coastal site grew significantly more slowly than coastal plants (0.082 vs 0.165 $\text{cm} \cdot \text{mo}^{-1}$, respectively). Ammen plants grew significantly faster at the 15 m site where both groups of plants achieved similar rates of growth (0.129 - 0.156 $\text{cm} \cdot \text{mo}^{-1}$). Coastal plants grew slowest (0.038 $\text{cm} \cdot \text{mo}^{-1}$) at the 30 m Ammen site. Although Ammen plants grew at 0.066 $\text{cm} \cdot \text{mo}^{-1}$ at the 30 m site there was no significant difference between the two groups of plants. However, when growth rates at this site were compared in terms of linear increase per month, significant differences were evident, with the

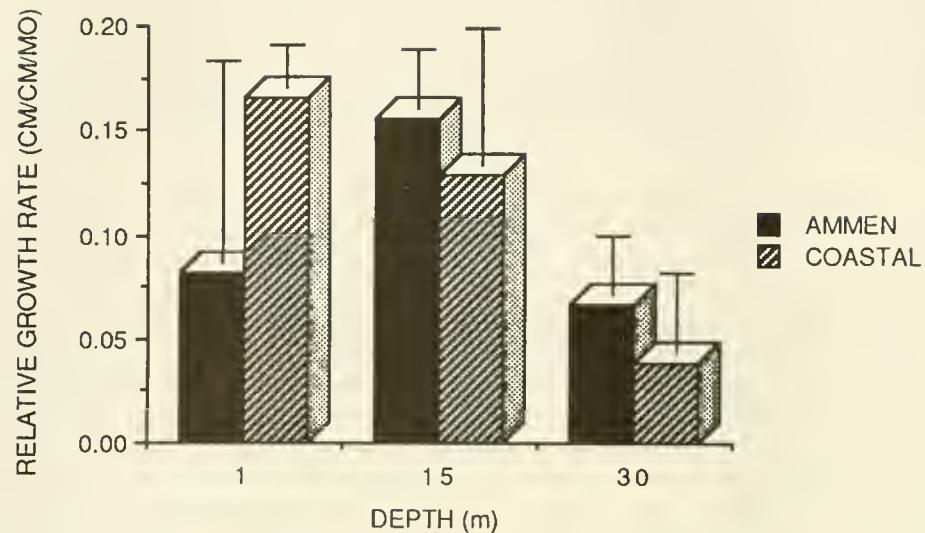


Figure 1. Relative growth rates of initial and transplanted Ammen and coastal *Laminaria*. Bars denote 95% confidence limits of mean ($n=5$).

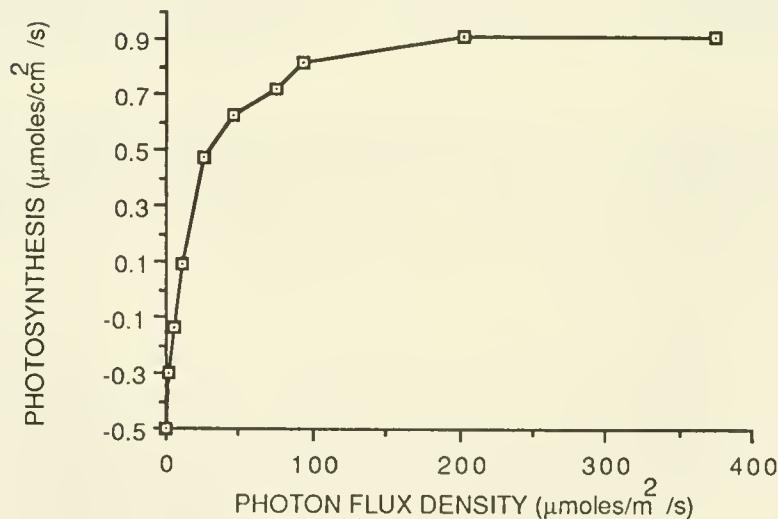


Figure 2. Representative data for photosynthesis versus irradiance response of coastal *Laminaria digitata* sampled June 1987.

Ammen plants increasing in length faster than the coastal group (4.38 vs 0.833 cm.mo⁻¹, respectively).

Figure 2 presents typical data for photosynthesis versus irradiance curves of coastal Laminaria digitata following the initial sampling of this population in June 1987. Similar curves were obtained for all groups of plants, although values for respiration, light compensation point, initial slope of the P vs I response (alpha) and light saturated rates of photosynthesis did vary between sites, and between plant group. These differences were compared by using the P vs I curves to calculate the following characteristics: respiration (umoles O₂. g f wt⁻¹.hr⁻¹): the mean oxygen consumption in the dark; alpha ([umoles O₂. g f wt⁻¹.hr⁻¹]/[umoles photons.m⁻².s⁻¹]): the slope of the initial, light limited region of the P vs I curve; P_{max} (umoles O₂. g f wt⁻¹.hr⁻¹): the average value of light saturated photosynthesis; I_k, the photon flux density required to just saturate photosynthesis (umoles photons.m⁻².s⁻¹): P_{max}/alpha; the light compensation point, where photosynthesis just balances respiration (umoles photons.m⁻².s⁻¹): calculated from alpha values and respiration rates.

Figure 3 presents data on the maximum rate of photosynthesis of the two groups of plants both initially and after growth at the three transplant sites. Initial P_{max} values were significantly greater for coastal Laminaria digitata than Ammen plants (0.806 vs 0.234 umoles.cm⁻².s⁻¹). The P_{max} of the coastal plants did not change significantly at any of the transplant sites. In contrast, Ammen plants transplanted to both the 1 and 15 m coastal sites and the 30 m Ammen site did exhibit considerable increases in P_{max} (to between 0.526 and 0.683 umoles.cm⁻².s⁻¹), although the rates were always lower than those of the coastal group.

Alpha values for the initial and transplanted plants are shown in Figure 4. Alpha values of coastal plants were significantly higher than those of the Ammen Laminaria in all cases except the 15 m coastal site. Alpha values were highest in the initial samples (0.052 and 0.035 [umole.cm⁻².hr⁻¹]/[umole photons.m⁻².s⁻¹] for coastal and Ammen plants, respectively) and lowest in the 30 m transplants (0.052 and 0.035 [umole.cm⁻².hr⁻¹]/[umole photons.m⁻².s⁻¹] for coastal and Ammen plants, respectively).

I_k values for photosynthesis are shown in Figure 5. There were no significant differences between the two groups of plants either initially or at any of the transplant sites. I_k values were lowest in the initial samples (7.21 and 15.60 umole photons.m⁻².s⁻¹ in Ammen and coastal plants, respectively) and highest at the 30 m transplant site (7.21 and 15.60 umole photons.m⁻².s⁻¹ in Ammen and coastal plants, respectively).

Figure 6 shows data for the light compensation points of Ammen and coastal Laminaria sampled initially in June 1987 and after growth at the transplant sites. With the exception of the

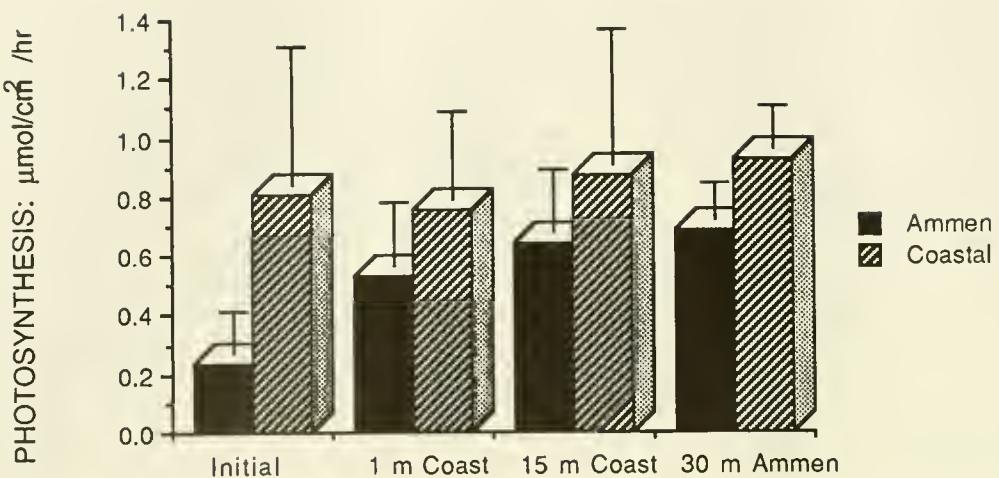


Figure 3. Maximum photosynthetic rates (P_{max}) of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

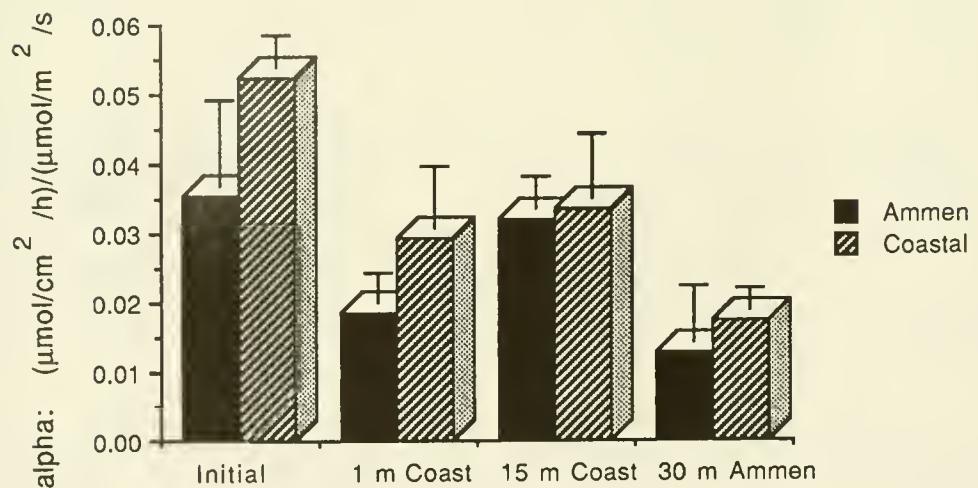


Figure 4. Alpha values of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

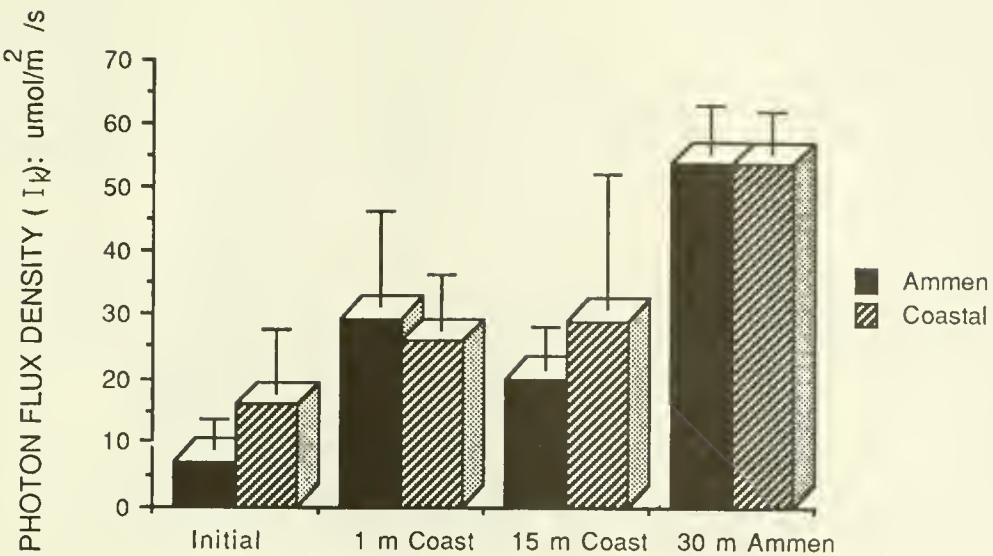


Figure 5. I_k values of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean (n=5).

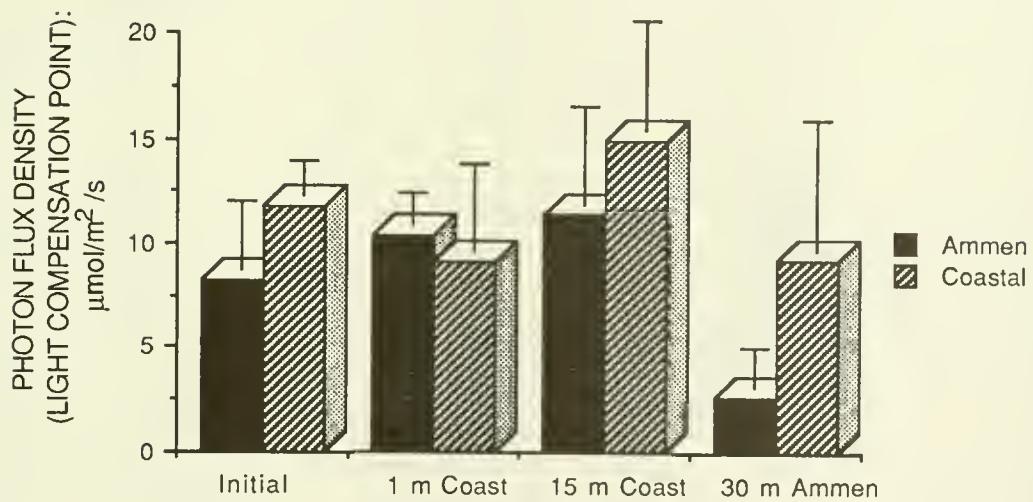


Figure 6. Light compensation points of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean (n=5).

1 m transplant site compensation points were always higher in coastal than Ammen plants, although the difference was only significant at the 30 m site. Significant differences did occur between the two plant groups when data for all of the sites were considered together. The only significant difference within either of the groups of plants with respect to depth was in the Ammen plant at the 30 m site, which had much lower compensation points than those for this group at any other site (2.61 vs 8.26-11.37 umole photons.m⁻².s⁻¹, respectively).

Figure 7 presents data on the rates of respiration of the Ammen and coastal plants. In all cases the respiration rates of coastal plants were higher than those for the Ammen group. However, these differences were only significant for the initial samples and when the data for all sites were pooled.

Figure 8 shows RUBISCO activities of the two groups of plants following initial sampling and after growth at the transplant sites. Significant differences occurred between the two groups of plants both initially and at the 30 m site, with coastal plants having higher values than the Ammen group. RUBISCO activities of the coastal Laminaria were 20.96 and 44.04 nmoles.g f wt⁻¹.min⁻¹ initially and at 30 m, respectively, while those of the Ammen plants were 10.35 and 13.36 nmoles.g f wt⁻¹.min⁻¹ initially and at 30 m, respectively. RUBISCO activities declined in both groups of plants transplanted to the 1 and 15 m coastal sites and did not differ significantly between the two groups being approximately 3.00 nmoles.g f wt⁻¹.min⁻¹ in all cases.

Figures 9, 10, and 11 present data on cellular concentrations of photosynthetic pigments (chlorophyll a, chlorophyll c and fucoxanthin, respectively) in Ammen and coastal Laminaria. With the exception of the 15 m site, coastal plants had significantly more chlorophyll a than the Ammen group (Figure 9). Highest chlorophyll a levels were found in the initial, June 1987, samples (0.353 and 0.661 ug.cm⁻² in Ammen and coastal plants, respectively) and lowest values in the 30 m site (0.137 and 0.321 ug.cm⁻² in Ammen and coastal plants, respectively), with intermediate levels occurring at the 1 and 15 m coastal sites. Chlorophyll c (Figure 10) and fucoxanthin (Figure 11) levels did not differ significantly either between sites or between the two plant groups with the exception of fucoxanthin in coastal Laminaria which were initially higher than those of Ammen plants (0.369 and 0.201 ug.cm⁻², respectively).

Figure 12 shows calculated rates of net carbon fixation in the Ammen and coastal Laminaria populations over a range of daily photon flux densities supplied in a 20:4 L:D photoperiod. Rates were calculated from measured rates of respiration and instantaneous P vs I responses assuming that total daily irradiance was averaged equally over the entire photoperiod. Calculated rates of net carbon fixation were greater in Ammen plants than the coastal population below a photon flux density

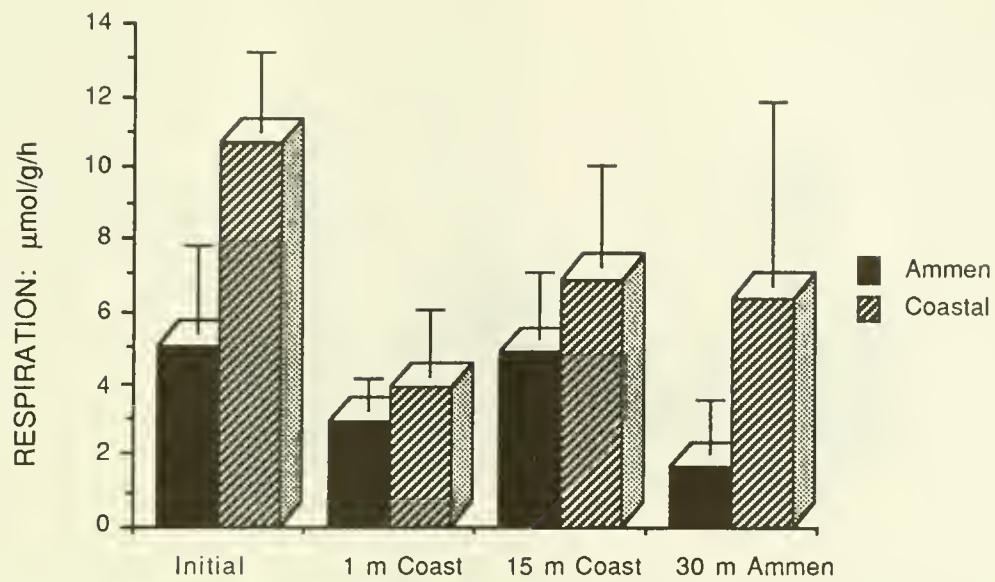


Figure 7. Respiration rates of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

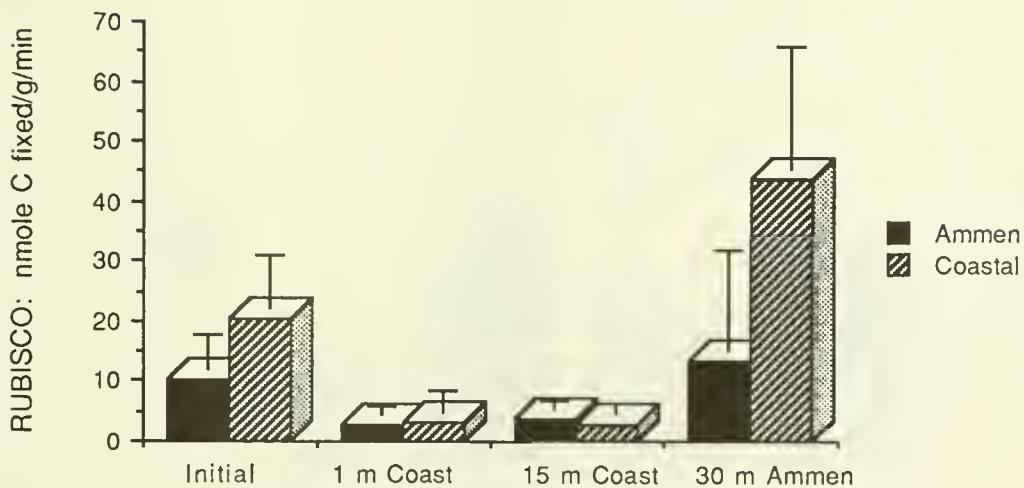


Figure 8. Activities of RUBISCO in initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=3$).

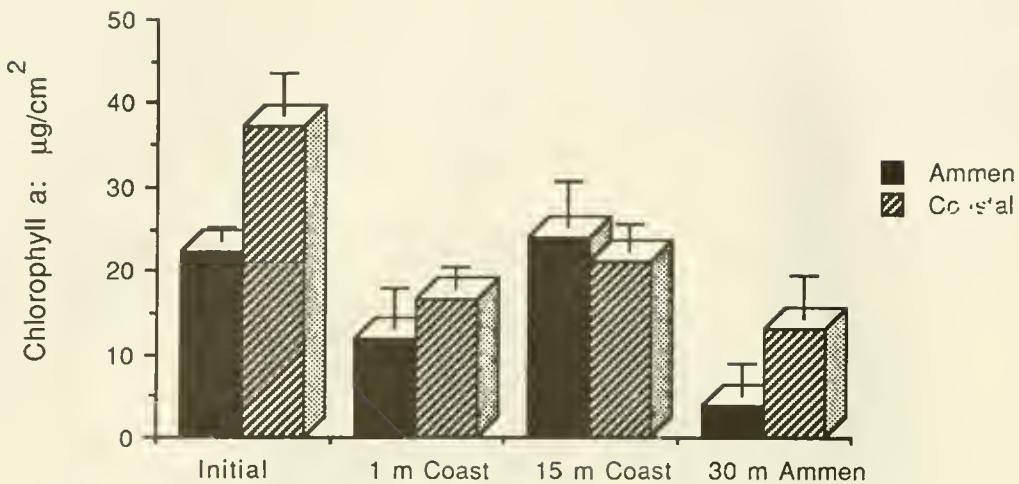


Figure 9. Chlorophyll a content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=3$).

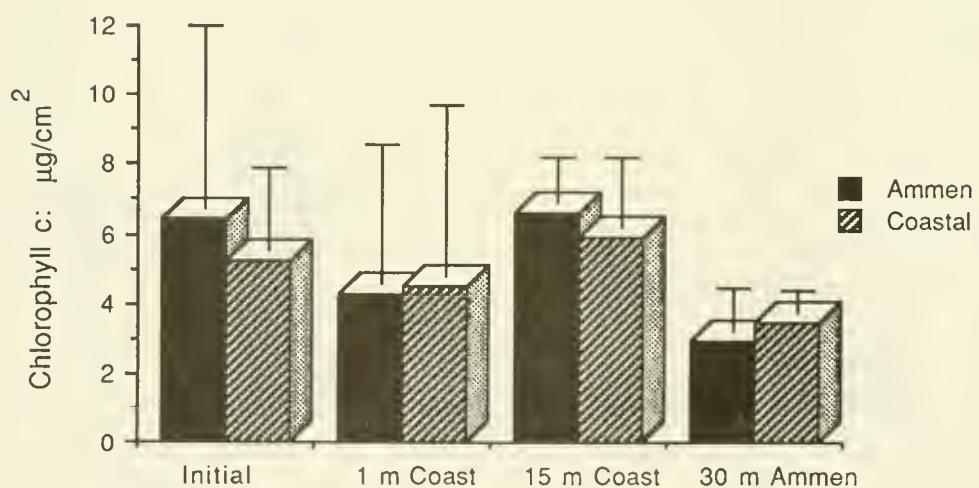


Figure 10. Chlorophyll c content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

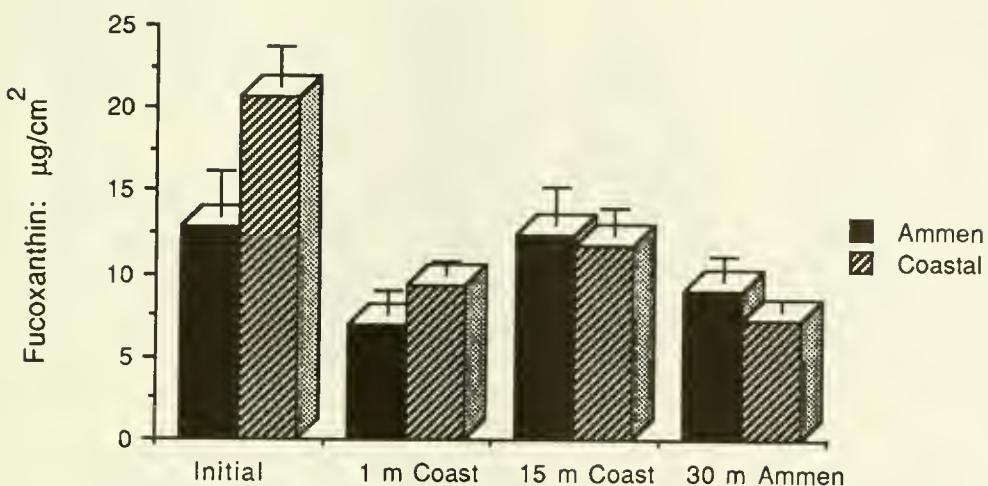


Figure 11. Fucoxanthin content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

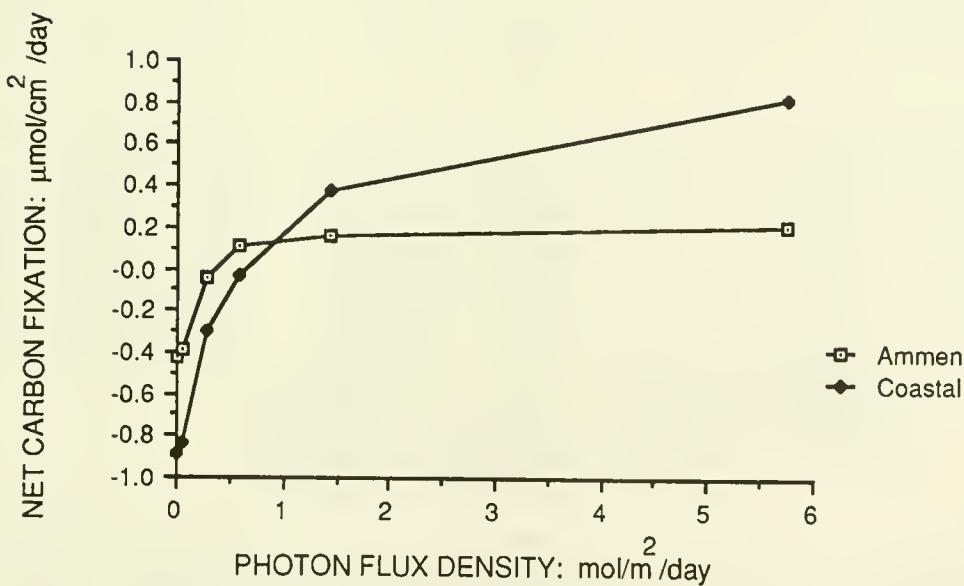


Figure 12. Calculated net daily carbon fixation of Ammen and coastal Laminaria based on data for initial (June) sampling period. This calculation assumes 20:4 L:D photoperiods with different average daily photon flux densities.

of 1.0 umole photons.m⁻².day⁻¹, with Ammen plants achieving net photosynthesis at a photon flux density (0.576 mole photons.m⁻².day⁻¹, 10 umole photons.m⁻².s⁻¹) at which coastal plants experienced a net carbon loss. Above 1 mole photons.m⁻².day⁻¹ the coastal plants achieved higher rates of net carbon assimilation than Ammen Laminaria. Similar patterns were obtained from the P vs I data of the 1, 15, and 30 m transplanted plants (data not shown).

Figures 13, 14, and 15 respectively show the cellular contents of mannitol, amino-N and nitrate in the Ammen and coastal Laminaria initially and following growth at the transplant sites. Initial mannitol levels in the Ammen plants were low (13.58 umole.g f wt⁻¹), whereas those for the coastal Laminaria were high (281.0 umole.g f wt⁻¹). Ammen plants transplanted to the 1 and 15 m coastal sites exhibited considerable increases in cellular mannitol levels to between 350 and 410 umole.g f wt⁻¹, whereas those at the 30 m Ammen site had much smaller increases in mannitol (62.4 umole. g f wt⁻¹). Mannitol levels in the coastal plants remained high at all transplant sites and did not differ significantly from the initial value. Initial amino-N levels were much higher in the coastal than Ammen Laminaria (40.96 cf. 10.92 umole.g f wt⁻¹, respectively) (Figure 14). Amino-N levels were lower in the 1 and 15 m coastal sites and did not differ significantly between the groups. At the 30 m site the Ammen plants had higher levels of amino-N than the coastal group (14.35 cf. 8.61 umole.g f wt⁻¹, respectively). Nitrate contents were undetectable in the coastal Laminaria population at all sites except for the 30 m transplants which had 1.95 umole.g f wt⁻¹. In contrast the initial Ammen plants had an initial cellular nitrate pool of 3.12 umole.g f wt⁻¹ which increased to 59.11 umole.g f wt⁻¹ at the 30 m site but which was lost at the 1 and 15 m coastal transplant sites.

Cellular nitrate reductase activities of the Laminaria plants are shown in Figure 16. Initially, coastal plants had significantly higher activities of this enzyme than Ammen plants (0.348 cf. 0.043 umole.g f wt⁻¹.hr⁻¹, respectively). Activities were similar at the 1 and 30 m transplant sites (0.126-0.156 and 0.025-0.031 umole.g f wt⁻¹.hr⁻¹ at 1 and 30 m, respectively) but were different at the 15 m site where Ammen plants had very low activities (0.007 umole.g f wt⁻¹.hr⁻¹) compared to the coastal group (0.092 umole.g f wt⁻¹.hr⁻¹).

DISCUSSION

The results presented here suggest that genetic differences do exist in the photosynthetic physiology of Ammen and coastal Laminaria plants. Overall, Ammen plants have lower maximum rates of photosynthesis (Fig. 3), lower respiration rates (Fig. 7) and lower light compensation points (Fig. 6) than the coastal L. digitata population. These differences persisted in transplanted plants, grown under similar light conditions, suggesting either

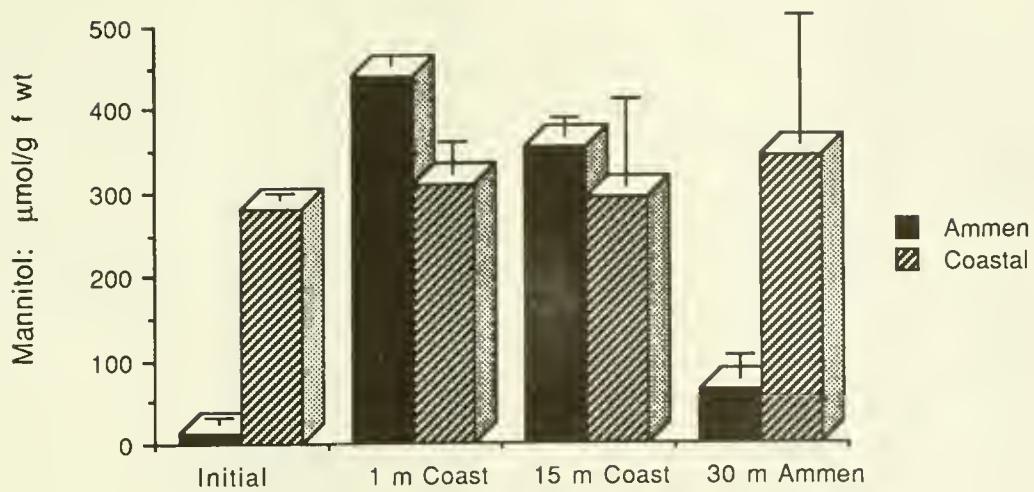


Figure 13. Cellular mannitol content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

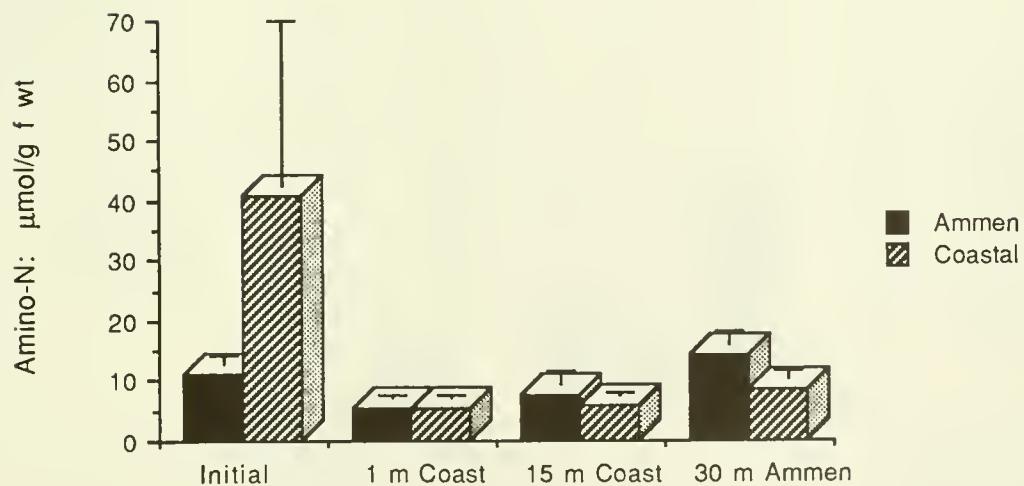


Figure 14. Cellular amino acid content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

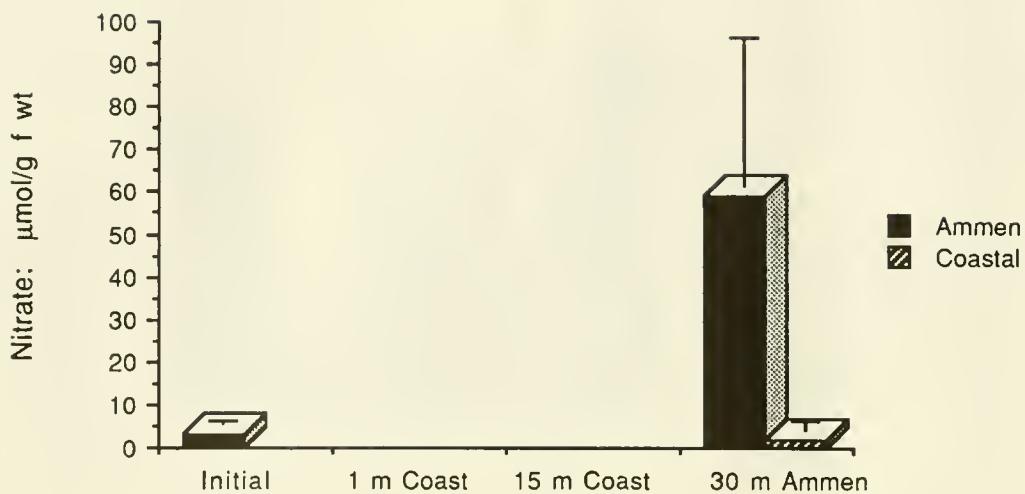


Figure 15. Cellular nitrate content of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=5$).

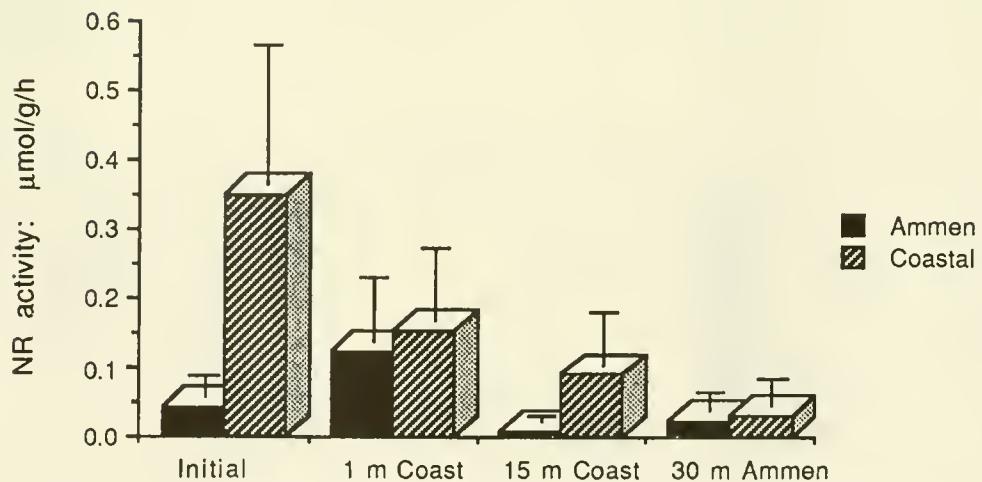


Figure 16. Potential nitrate reductase activity of initial and transplanted Ammen and coastal Laminaria. Bars denote 95% confidence limits of mean ($n=3$).

that the Ammen population is a low irradiance ecotype of L. digitata, or if a distinct species, one which has evolved adaptations to cope with low irradiance levels. Ecotypes of Laminaria species have previously been documented both for nitrogen (Espinoza and Chapman, 1983) and irradiance (Gerard, 1988). The adaptive significance of the differences in the photosynthetic characteristics between Ammen and coastal Laminaria is evident from a consideration of the predicted net photosynthesis achieved at different light levels (Fig. 12). By virtue of their lower respiration rate and compensation point, Ammen plants would achieve greater rates of net photosynthesis (and hence growth) than the coastal group at low photon flux densities. In contrast, coastal L. digitata would grow faster than Ammen plants at photon flux densities above 1 umole photons. $m^{-2}.s^{-1}$. The predicted responses are supported by the growth data, which indicate that the coastal plants did grow fastest in the high irradiance, 1 m coastal site, whereas Ammen plants grew faster in the lower light environments of the 15 m and 30 m sites (Fig. 1). Because of the reduction in photosynthesis and stimulation of respiration associated with wounding (Gerard, 1988), the calculated photon flux densities required to achieve net photosynthesis (Fig. 12) are probably higher than those required in nature by intact plants. However, assuming the two groups of plants exhibit similar responses to wounding, this does not affect the interpretation of the data.

Somewhat surprisingly, coastal L. digitata plants were more efficient at utilizing low light levels than the Ammen population (Fig. 4). The increase in alpha did not however compensate for the increased respiration rates of the coastal plants. The increase in alpha of the coastal plants was probably due to the higher chlorophyll contents of these plants (Fig. 9). There was a strong correlation between alpha and content of chlorophyll a for both plant groups (correlation coefficient 0.975), suggesting that much of the additional chlorophyll was in the form of antenna pigments in the photosynthetic units. The lower respiration rates characteristic of the Ammen population suggests that these plants invest less energy in cell maintenance and biosynthesis than the coastal L. digitata. This would explain the lower chlorophyll a contents and enzyme activities of the Ammen population (Figs. 8, 9, and 16), all of which would enable these plants to conserve energy required for the biosynthesis of these molecules, but which restrict P_{max} and hence growth at high light levels.

The initial biochemical composition of the two plant groups suggest that the coastal L. digitata population was nitrogen limited (absence of cell nitrate and presence of large mannitol pool; Figs. 13 and 15) whereas the Ammen plants were not (Davison et al., 1984). The reduction in cellular amino-N content (Fig. 14) and enzyme activities (Figs. 8 and 16) together with a slight increase in mannitol pool (Fig. 13) indicates that nitrogen limitation became more severe for the coastal plants during the period that they were transplanted at the 1 and 15 m site (Wheeler and Weidner, 1983; Davison et al., 1984). The Ammen plants at

this site also exhibited symptoms of nitrogen limitation. In contrast, Ammen Laminaria at the 30 m site exhibited a considerable increase in cellular nitrate (Fig. 15), and retained a relatively small pool of mannitol (Fig. 13), suggesting that light rather than nitrogen was the limiting factor at this site. The inability of coastal L. digitata to utilize the inorganic nitrogen available at the Ammen site (Fig. 15) suggests that these plants were severely energy limited.

Overall, the data in this paper support the idea that the Ammen Laminaria population is genetically different from the coastal population of L. digitata which it closely resembles. The Ammen population seems well adapted to life in a low irradiance environment. However, caution is necessary when interpreting these results for two reasons: First, the plants used were mature sporophytes and it is possible that the observed responses reflected their exposure to previous growth conditions rather than responses to conditions during the transplant experiments. Second, although reciprocal transplants were used to study the response to light, it is clear that other environmental factors (especially nitrogen availability) influenced the results. Because of this, the differences in the photosynthetic physiology of the two groups of plants have been investigated in more detail under controlled laboratory conditions. These results will be presented elsewhere.

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EARLY COMMUNITY DEVELOPMENT EXPERIMENTS IN ROCKY SUBTIDAL
HABITATS (GULF OF MAINE, 30-80 M)

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ABSTRACT

Sessile invertebrates dominate rocky subtidal communities at depths greater than 30 m, and vertical rock surfaces as shallow as 5 m in the Gulf of Maine. At Cashes Ledge, in the outer Gulf of Maine, sponges, sea anemones, bryozoans and ascidians make up most of the invertebrate community on vertical surfaces at 30 m and become abundant on horizontal and sloping surfaces below that depth. A decrease in water movement and an increase in sediment accumulation on rocks deeper than 50 m may affect both recruitment and growth of sessile species. In 1985 we began a series of experiments to compare colonization of vertical surfaces (roughened plexiglas plates) placed at depths of 30, 50, 65 and 80 m on Ammen Rock Pinnacle, part of the Cashes Ledge formation. All settling plate racks had one set of plates oriented outward and another oriented inward, thus experiencing reduced water flow. Panels with settling plates were collected one year later and the composition of the encrusting community on their surface was analyzed. At 30 m plate surfaces were dominated by encrusting bryozoans, inner and outer surfaces had approximately equal cover of encrusting and erect bryozoans, and unoccluded space was less than 10%. At 50 m both inner and outer plate surfaces were colonized primarily by the erect bryozoan species and unoccluded space was approximately 30% on the inner and outer surfaces. Unoccluded space accounted for 45-70% of the area on inner and outer plates at 65 m, and 60-70% at 80 m depths. Bryozoans were by far the majority of species at all depths except at 80 m where the polychaetes Filograna implexa and Spirorbis spp. equalled their abundance. The most common erect bryozoan, the cyclostome Idmidronia atlantica, reached its greatest percent cover at 50 m decreasing above and below that depth. This species alone accounted for much of the distinct pattern of erect bryozoan cover with depth. Our preliminary results show a pattern of decreasing rate of space colonization with increasing depth for all bryozoan species combined, probably as a result of differences in recruitment, survivorship, and/or growth rates over the year. The lesser abundance of erect bryozoans at 30 m, especially on the outer plates, argues that water movement may be too strong at that depth to allow these fragile species to grow well here. The decreasing percent cover of all sessile species with depth may be due to either lower food

availability, less water flow, or larval scarcity as depth increases.

INTRODUCTION

Benthic assemblages inhabiting rock surfaces often take many years to develop on initially cleared rock or other hard surfaces (Osman, 1977, 1978; Sebens, 1985, 1986; Paine and Levin, 1981). The time scale of recolonization depends on the availability of propagules of the component species, their advection toward the substratum, and on their interactions with species already inhabiting the surface. Most studies of epifaunal encrusting community development have been conducted in shallow water temperate habitats (Karlson, 1978; O'Connor, et al. 1980; Kay and Keough, 1981; Sebens, 1985, 1986) or on the undersides of coral plates in cryptic reef habitats (Jackson, 1977a,b, 1979; Buss and Jackson, 1979; Buss, 1980). Colonization of artificial or natural surfaces in deeper water, and the type of assemblages that develop, are virtually unknown.

Experiments in early community development often employ artificial plates constructed of plastic, rock, asbestos or other suitable material, frequently roughened to enhance successful larval settlement and adhesion (Sutherland, 1975; Sutherland and Karlson, 1971; Schoener, 1974; Schoener et al., 1979; Shin, 1981; Harris and Irons, 1982). Such plates are easy to monitor because of their flat surfaces and identical sizes. They are, however, usually separated from the substratum and thus from certain benthic predators which could influence community processes. On the other hand, they are also separated from adjacent sessile species which could colonize plates by lateral growth. Suspended plates thus sample recruitment (minus mortality) of species with larvae in the water column just above the bottom. Alternatively, other studies have used scraped natural surfaces in contact with the adjacent substratum and its occupants (Dayton, 1971, 1975; Kay and Keough, 1981; Sebens, 1985, 1986; Witman 1987). This method has the advantage of allowing all normal community effects to influence settlement, recruitment, and subsequent growth and survival of colonists. However, it is then difficult to distinguish colonization from the water column from lateral growth or asexual proliferation by adjacent encrusting species. Also, scraped areas often retain some fragments of colonies or algal thalli within small crevices, and thus there is another source of recolonization. It has been argued that this method mimics naturally occurring patches more closely than do any of the artificial substratum methods. Finally, at least one study conducted in the rocky intertidal zone followed naturally created patches of a wide size range for several years, quantifying the changes in patch size and occupants (Paine and Levin 1981).

In the present study, we used a number of different experimental techniques to explore early community development at four depths (30, 50, 65, 80 m) along a transect down the slope of Ammen Rock Pinnacle, on Cashes Ledge in the center of the Gulf of

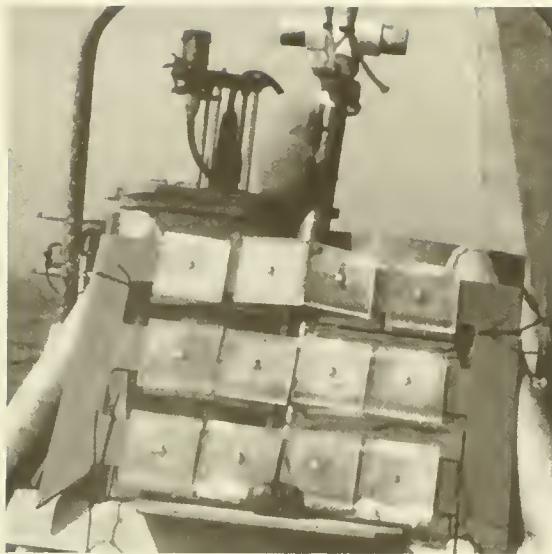
Maine (see Witman and Sebens 1988). These experiments included artificial plates, granite slabs and blocks, artificially created patches on rock wall surfaces, and natural patches in monitored quadrats on rock walls. The purpose of this set of experiments was to determine which species make up the early successional assemblage and to find out how they occupy space and interact with each other as a function of depth. In addition, we explored the effects of substratum angle, large predator exclusion, and water flow on the early stages of community development. Some of the experiments have run for over two years to date, and we expect to monitor them for several more years to determine how long the entire process of community development must proceed before all or most of the characteristic species have become established. In this report, we present data from our first year of settling plate experiments and we discuss the design of our overall experimental study of community development.

METHODS

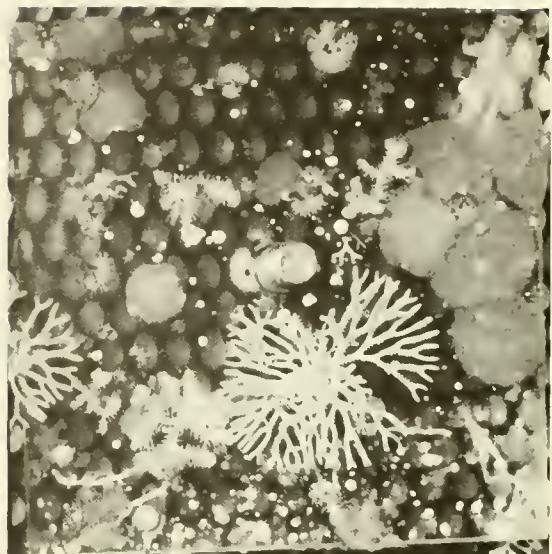
Artificial Settlement Panels

In July 1985 we deployed concrete bases with upright PVC corner pipes slit vertically so that settling plate racks could be slid into place and removed easily using the mechanical arm of the Johnson Sea Link submersible. Each removable rack held twelve panels on its outer and inner surfaces, the inner surface receiving somewhat less water movement and the outer surface being exposed to ambient currents without obstruction (Fig.1). Plates (7.5 x 7.5 cm) were constructed of 6 mm thick plexiglas roughened on both sides using sandpaper. They were attached to the rack with a central stainless steel nut and bolt through holes in both inner and outer panels at any one position on the rack. Panels thus formed a square surface approximately 34 cm on a side, with 0.5 cm between plate edges. Completed racks were delivered to the bottom stations on concrete bases (Depth-Specific-Research-Station, or DRS) using the Johnson Sea Link submersible and were placed in position with the mechanical arm. At the 30 and 50 m stations, small cable ties were used to secure the racks to the DRS to prevent movement by wave surge. Racks at 30 m depth were placed and removed by SCUBA divers.

Racks of panels were collected the following year using the submarine's mechanical arm to lift each rack by a T-handle on top and then to turn the rack so that it faced the front rack of the submersible on which a Hasselblad camera with a framer rack was mounted. The framer allowed positioning of the plate rack so that it was completely in view and in focus. Film was 6 x 6 cm format Ektachrome color transparency film, which gave excellent resolution for each plate in the rack. Racks were then placed individually in the front collecting basket of the submersible, positioned so that plate surfaces were free of any contact. Once brought back to the surface, plate racks were immediately immersed in flowing seawater containers for 6-48 hrs. Six panels were removed from each side of each plate rack, photographed



A



B

Figure 1.

A. Fouling panel rack containing 12 roughened plexiglass plates (56.25 cm^2 area) on each side (inner and outer) of rack on bow of Johnson Sea Link submersible. Each rack was inserted into a Depth-specific Research Station (DRS) at 30, 50, 65, and 80 m depth.

B. Close up of one fouling plate after one year of colonization at 50 m depth. Bryozoan species are Idmidronea atlantica (erect, fan-shaped), Tubulipora lillacea (left of Idmidronea), encrusting species are probably Schizomavella auriculata. Serpulid polychaete is Spirorbis spp.

individually using 35 mm Kodachrome 64 film, then preserved in buffered formalin in seawater and transferred to 70% ethanol after several days for long-term storage. We noted that the erect fan-shaped, bryozoan Idmidronea atlantica did not survive transport and handling very well; the initial Hasselblad photos were thus the only accurate record of its abundance. After storage, Idmidronea was removed by clipping each colony just above its small encrusting base. Plates were photographed again, this time using black and white Panatomic X film in the laboratory.

Abundances of individual species on the collected plates were quantified by tracing outlines of the colonies or individuals on clear plastic overlays of the final black and white photos, digitizing the outline on an Apple II microcomputer with graphics tablet digitizer, then using the Apple II program to calculate surface area of the colony (method in Sebens 1986). Once the tracing map was complete, the shipboard 35 mm photographs were projected onto the tracings to determine if any colonies had been lost during transport and storage. Any that appeared were then traced onto the final map. Imidronea atlantica was traced on paper from the original Hasselblad photographs; the area circumscribed by the branch tips was digitized and calculated in the same manner. The tube-worms Spirorbis spp. were counted directly on each plate, then a subsample of 20 individuals was digitized for surface area and counts were converted to area where needed. Total bare space on panels was calculated by overlaying a grid of 200 randomly placed 2 mm circles on the final outline map of the plate and counting the number of dots that fell on unoccupied space (method in Sebens 1986). Another category of 'unoccluded space' was defined as the amount of bare space that was not also covered by the canopy of Idmidronea, which usually reached down to within a millimeter or two of the substratum. This was also determined using 200 random circles. All percent cover values were arcsine-transformed for calculation of mean and standard deviation. Differences between inner and outer groups and between depths were tested with Analysis of Variance followed by Student-Newman-Keuls Multiple Comparison Test (Sokal and Rohlf, 1969). Bryozoan species were identified using several sources, primarily Osburn (1910) and Rogick and Croasdale (1949). In addition to the plates collected after one year, the other twelve plates per rack were returned to the appropriate DRS and twelve new plates were attached to record the second year's initial community development. Panels that were not removed were used to record the second and third year of community development.

Granite Blocks and Slabs

Granite blocks (15 x 30 x 10 cm approx. dimensions) were embedded two per concrete base with rope handles, then were placed at all depths (30, 50, 65, 80 m) in summer 1985. Upper surfaces of these blocks were photographed by SCUBA divers at 30 m and by the 35 mm camera on the Johnson Sea Link at all other

depths. Photographic sampling was repeated in summers of 1986 and 1987 and will be continued in the future (Table 1). In summer 1986, we constructed 24 concrete bases (40 x 40 x 10 cm approx. dimensions) each with two horizontal granite slabs and one or two vertical slabs (20-30 cm tall) per base. One side of each vertical slab was covered with a one cm mesh vexar cage (15 x 15 x 5 cm) to exclude large predators (3 replicates per depth). Three other vertical faces per depth were covered with the same type of cage but with two sides removed to allow predator access but to reduce water flow as in complete cages (cage control). Six other vertical surfaces were left unobstructed at each depth. These units were collected after one year (September 1987) and were photographed on all surfaces using a 35 mm camera and a macro lens (Kodachrome 64 film). In addition, all mobile fauna on each rock surface were collected and identified to determine if small predators were present that could affect the community development.

Patches on Rock Walls

A series of artificially scraped patches were created in summer 1987 by SCUBA divers using a knife and wire brush to remove all encrusting species in patches 10 x 10 cm on natural rock walls at 30 m depth (method in Sebens 1986). Even heavy brushing does not remove all crustose algal thalli or pieces of invertebrate colonies wedged in small crevices. However, community development in such patches mimics that in natural patches and the early successional community that develops is subject to the same influences as are natural patches, including the effects of larger benthic predators that are unlikely to climb onto settling plate racks. These experiments will be monitored twice annually for as many years as possible into the future.

In 1985 we began photographing a series of 10 unmanipulated 0.25 m^2 quadrats on rock walls at 30 m using a Nikonos camera with 15 mm wide angle lens, mounted on an aluminum quadrapod (Witman 1985). Natural mortality of sponges, sea anemones, and other encrusting species has been observed in these quadrats. Subsequent photographs will determine the nature of early community development in these natural patches as well, for comparison to results in artificial patches and on settling panels.

RESULTS

The first year's community development on settling panels was striking in several aspects. Panels at the shallowest station (30 m) were almost completely covered with erect and encrusting bryozoans (19 species, Table 2), as were the panels from the next depth (50 m) which had 14 species (Figures 2-5). Panels from the deeper two stations were far less heavily encrusted and had smaller numbers of bryozoan species (13 at 65 m, 12 at 80 m). Encrusting bryozoans were most abundant at the

Table 1. Design of recruitment and community development experiments. Settling plates are held on vertical rocks separated from the substratum, granite blocks are in contact with the substratum and are thus available to all benthic predators. N = no. replicates per depth, C = collected, S = sampled, F = future collection.

Experiment (all depths unless noted)	N	Dates Run	Dates Collected or Sampled
Settling plates, yr. 1 (7.5 x 7.5 cm)	24	July 1985-1988	1985 (C) 1987 (S)
Settling plates, yr. 2 (7.5 x 7.5 cm)	12	July 1986-1988	1987 (C)
Settling plates, yr. 3	12	Sept. 1987-1988	(F)
Granite blocks I (horiz.) (15 x 30 cm)	3	July 1985-1988	1986 (S) 1987 (S)
Granite blocks II (horiz.) (caged/uncaged) (vert.) (20 x 20 cm)	6	July 1986-1988	1987 (C)
Granite blocks III (horiz.) (vert.) (20 x 20 cm)	4	Sept. 1987-1988	(F)
Artificial wall scrapings (10 x 10 cm) 30 m only	10	June-Sept. 1987	(F)

Table 2. Abundance of sessile invertebrate species colonizing roughened plexiglass plates (7.5 x 7.5 cm) at Ammen Rock Pinnacle. Plates were immersed for one year at 30, 50, 65, and 80 m depth. Data presented as mean values \pm one standard deviation (n = 6 plates/depth) on arcsine transformed data (mean - sd, mean + sd).

BRYOZOA TABLE

SPECIES	MEAN % COVER - INNER PLATES				80 M
	30 M	50 M	65 M	80 M	
<i>Idmidronea atlantica</i>	23.69(5.81,48.78)	53.09(29.99,75.50)	28.21(8.16,54.45)	2.51(0.46,14.19)	
<i>Tubulipora liliacea</i>	12.27(6.65,19.3)	3.95(2.74,5.36)	2.55(1.15,4.47)	0.5(0.02,2.31)	
<i>Tubulipora flabellaria</i>	0.2(0.0004,0.8)	1.97(0.19,5.53)	0.47(0.03,1.42)	0.18(0.003,0.8)	
<i>Caberea ellisii</i>	0.04(0.0,0.39)	0.004(0.004,0.04)	0.002(0.002,0.02)	0.06(0.0,0.66)	
<i>Crisia eburnea</i>	0.05(0.0,0.56)	0	0	0	
<i>Porella proboscidea</i>	2.89(0.28,8.12)	0.09(0.09,0.84)	0.008(0.0,0.08)	0.003(0.0,0.03)	
<i>Porella propinqua</i>	0	0	0	0.008(0.0,0.89)	
<i>Porella concinna</i>	0.05(0.0,0.55)	0	0	0	
<i>Callopora aurita</i>	1.17(0.001,4.48)	0.07(0.07,0.62)	0	0	
<i>Callopora craticula</i>	2.08(0.004,8.49)	0.91(0.09,2.53)	0.91(0.14,2.36)	0.64(0.0009,2.45)	
<i>Callopora lineata</i>	4.91(0.17,15.54)	0	0	0	
<i>Schizomavella auriculata</i>	0	0.79(0.02,3.65)	0.08(0.0,0.8)	0.08(0.05,0.6)	
<i>Celleporella hyalina</i>	19.06(11.22,28.39)	0	0	0.02(0.0,0.26)	
<i>Cylindroporella tubulosa</i>	0.71(0.24,1.44)	0	0	0	
<i>Lichenopora hispida</i>	0.08(0.0002,0.32)	0.18(0.009,0.56)	0.18(0.0001,0.71)	0	
<i>Lichenopora verrucaria</i>	0.19(0.01,0.56)	0	0.01(0.0,0.12)	0.29(0.01,0.95)	
<i>Haplota clavata</i>	0.02(0.0,0.21)	0.004(0.004,0.04)	0	0.03(0.02,0.23)	
<i>Lepralia americana</i>	0	0.05(0.05,0.44)	0	0.92(0.46,1.55)	
<i>Rhamphostomella costata</i>	0	0	0	0.09(0,1.06)	
<i>Liripora amphorae</i>	0.008(0.0,0.08)	0.15(0,1.6)	0	0	
<i>Filograna implexa</i>	0	0	3.46(0.28,9.98)		
				MEAN NUMBER	
<i>Spirorbis</i> spp.	64.88(36.71,100.93)	213.19(112.34,345.98)	53.73(28.46,86.85)	114.51(59.21,187.78)	
<i>Anomia</i> sp.	0	0	0.23(0.25,0.96)	1.44(0.53,2.65)	

Table 2. Continued

BRYOZOA TABLE

SPECIES	MEAN % COVER - OUTER PLATES				MEAN NUMBER
	30 M	50 M	65 M	80 M	
<i>Idmiodonea atlantica</i>	6.27(0.04,21.80)	32.13(14.07,53.51)	12.0(6.16,19.46)	1.28(0.003,4.34)	
<i>Tubulipora liliacea</i>	23.87(17.22,31.22)	5.9(1.96,11.77)	2.67(1.44,4.27)	0	
<i>Tubulipora flabellaris</i>	0.55(0.0005,2.12)	1.93(1.17,2.87)	0.26(0.03,0.74)	0	
<i>Caberlea ellisia</i>	0.03(0.05,0.3)	0	0.02(0.004,0.12)	0	
<i>Crisia eburnea</i>	0.06(0.0,0.77)	0	0	0	
<i>Porella proboscidea</i>	2.43(0.01,8.92)	0.005(0.005,0.04)	0.03(0.0,0.28)	0.004(0,0.05)	
<i>Porella propinqua</i>	0.04(0.0,0.46)	0.05(0.005,0.42)	0	0	
<i>Porella concinna</i>	0.36(0.16,2.55)	0.04(0.04,0.34)	0	0	
<i>Callopora aurita</i>	1.4(0.83,10.41)	0.02(0.02,0.14)	0.05(0.0,0.54)	0	
<i>Callopora craticula</i>	2.76(1.06,5.24)	1.93(0.31,4.88)	0.45(0.0005,1.72)	1.51(0.15,4.25)	
<i>Callopora lineata</i>	0.2(0.2,1.94)	0	0	0	
<i>Schizomavella auriculata</i>	0.03(0.0,0.39)	2.5(0.09,8.01)	0	1.61(0.19,4.39)	
<i>Celleporella hyalina</i>	21.69(14.51,29.87)	0	0	0	
<i>Cylindroporella tubulosa</i>	0.94(0.19,5.56)	0	0	0	
<i>Lichenopora hispida</i>	0.21(0.01,0.68)	0.08(0.004,0.27)	0	0	
<i>Lichenopora verrucaria</i>	0.43(0.14,0.89)	0.004(0.004,0.03)	0	0.04(0.001,0.18)	
<i>Haoliota clavata</i>	0	0.16(0.16,1.41)	0	0	
<i>Lepralia americana</i>	0.19(0.005,0.89)	0	3.22(1.66,5.28)	0	
<i>Rhaphostomella costata</i>	0	0	0.09(0,0.97)	0	
<i>Liripora amphorae</i>	0.09(0.03,0.59)	0	0.58(0.005,2.51)	0	
<i>Filograna implexa</i>	0.47(0.99,5.49)	0	0.28(0.03,0.77)	4.23(1.26,8.82)	
<i>Spirorbis spp.</i>	200.82(175.98,227.29)	211.94(144.24,292.59)	34.43(24.19,46.44)	139.01(102.32,181.28)	
<i>Anomia sp.</i>	0	0	0.13(0.16,0.51)	1.23(0.44,2.26)	

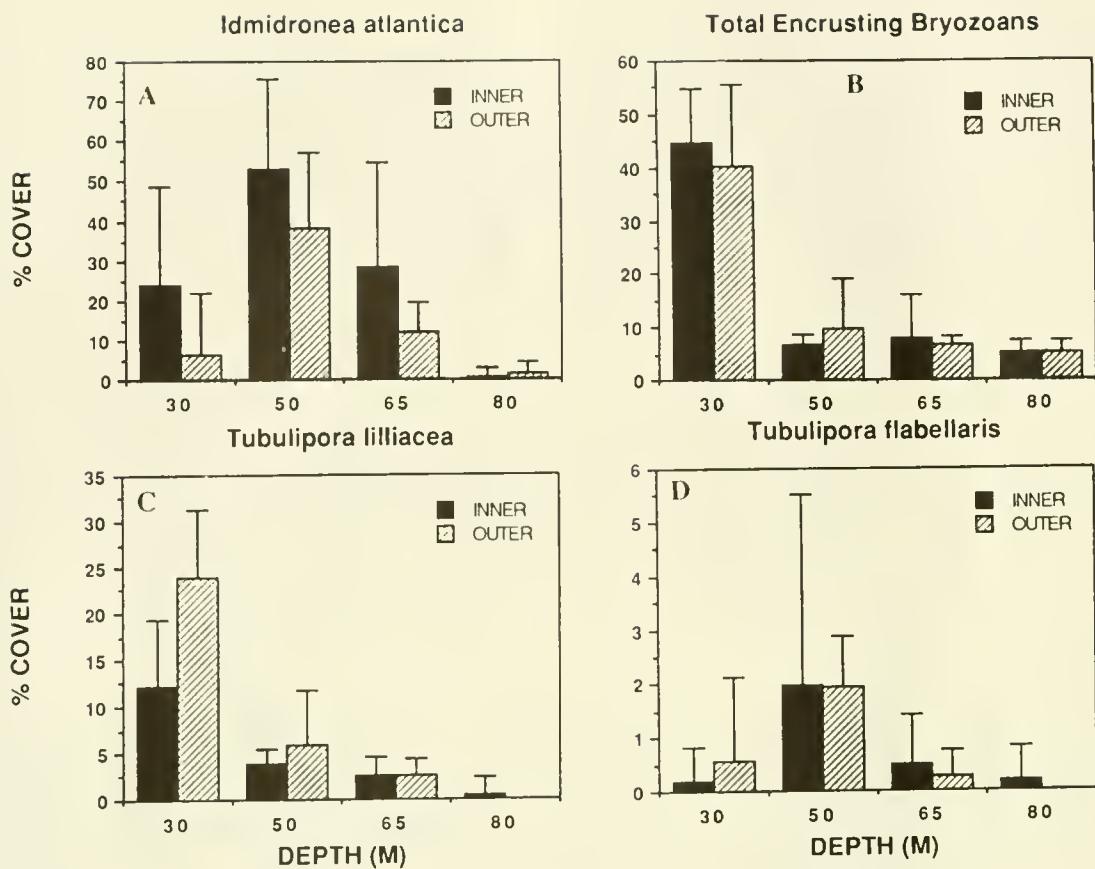


Figure 2.

A. *Idmidronea atlantica* percent cover at four depths. Inner plates had significantly greater cover (ANOVA, $p < 0.05$, 7, 33 df, $F = 8.8$) at 30, 50, and 65 m. All depths are significantly different from each other for both inner and outer groups.

B. All encrusting bryozoans percent cover at all depths, not including *Tubulipora lilliacea*. Samples at 30 m differ significantly from those at all other depths (ANOVA, $p < 0.05$, 7, 33 df, $F = 24.9$), but inner and outer groups are not different at any depth.

C. *T. lilliacea* percent cover at all four depths. Means at 30 m differ from each other significantly (ANOVA $p < 0.05$, 7, 33 df, $F = 31.1$, inner and outer) and each differs from means at all other depths. Means at 50 and 65 m also differ significantly from those at 80 m.

D. *T. flabellaris* percent cover at all four depths. Means at 50 m differ from those at 80 m only (ANOVA, $p < 0.05$, 7, 33 df, $F = 3.9$).

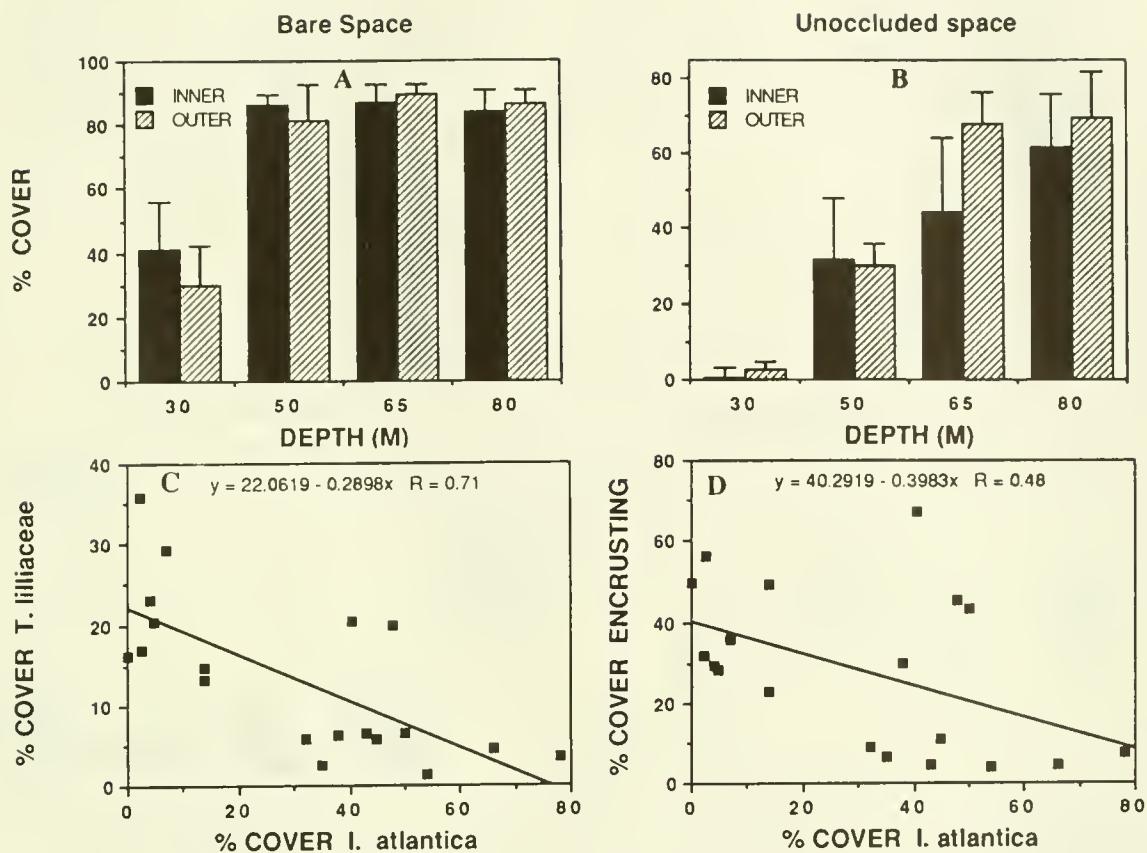


Figure 3.

A. Percent cover of bare space on all plates at four depths. Mean at 30 m differ significantly from those at 45, 65 and 80 m (ANOVA, $p < 0.05$, 7, 33 df, $F = 29.9$).

B. Percent cover of unoccluded space on all plates at four depths. This is space not covered by encrusting species or by branching canopies. Means at 30 m and 50 m differ significantly from those at 60 and 80 m (ANOVA, $p < 0.05$, 7, 33 df, $F = 38.9$).

C. Regression of *T. lilliaceae* percent cover as a function of *Idmidronea* cover ($y = 22.06 - 0.29x$, $R = 0.71$)

D. Regression of percent cover of all encrusting species pooled as a function of *Idmidronea* cover ($y = 40.29 - 0.40x$, $R = 0.48$)

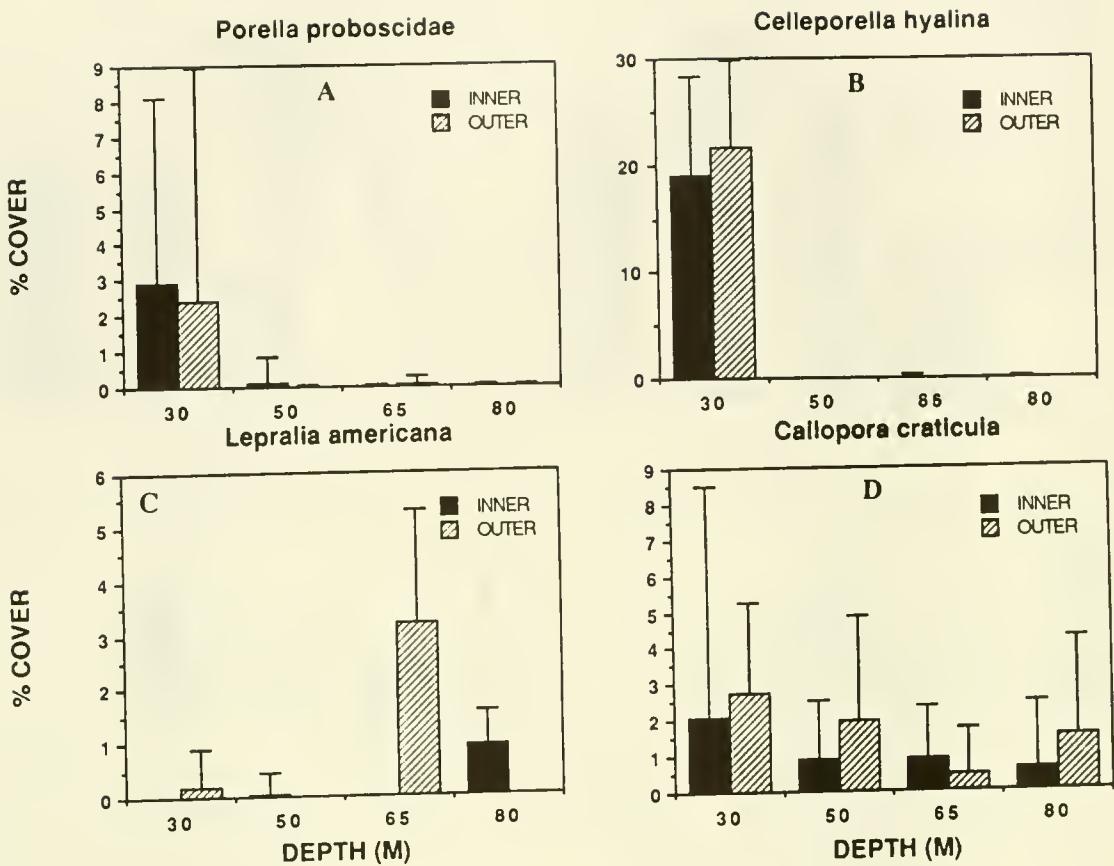


Figure 4.

A. Percent cover of Porella proboscidea at four depths. Means (inner and outer) at 30 m differ significantly from those at all other depths (ANOVA, $p < 0.05$, 7, 33 df, $F = 4.8$).

B. Percent cover of Celleporella hyalina at four depths. Means (inner and outer) at 30 m differ significantly from those at all other depths (ANOVA, $p < 0.05$, 7, 33 df, $F = 77.5$).

C. Percent cover of Lepralia americana at four depths. Mean (inner) at 80 m differs from all other means. Mean (outer) at 65 m differs significantly from all other means (ANOVA, $p < 0.05$, 7, 33 df, $F = 21.4$).

D. Percent cover of Callopora craticula at four depths. Means not significantly different for any group (ANOVA, $p > 0.05$, 7, 33 df, $F = 0.9$).

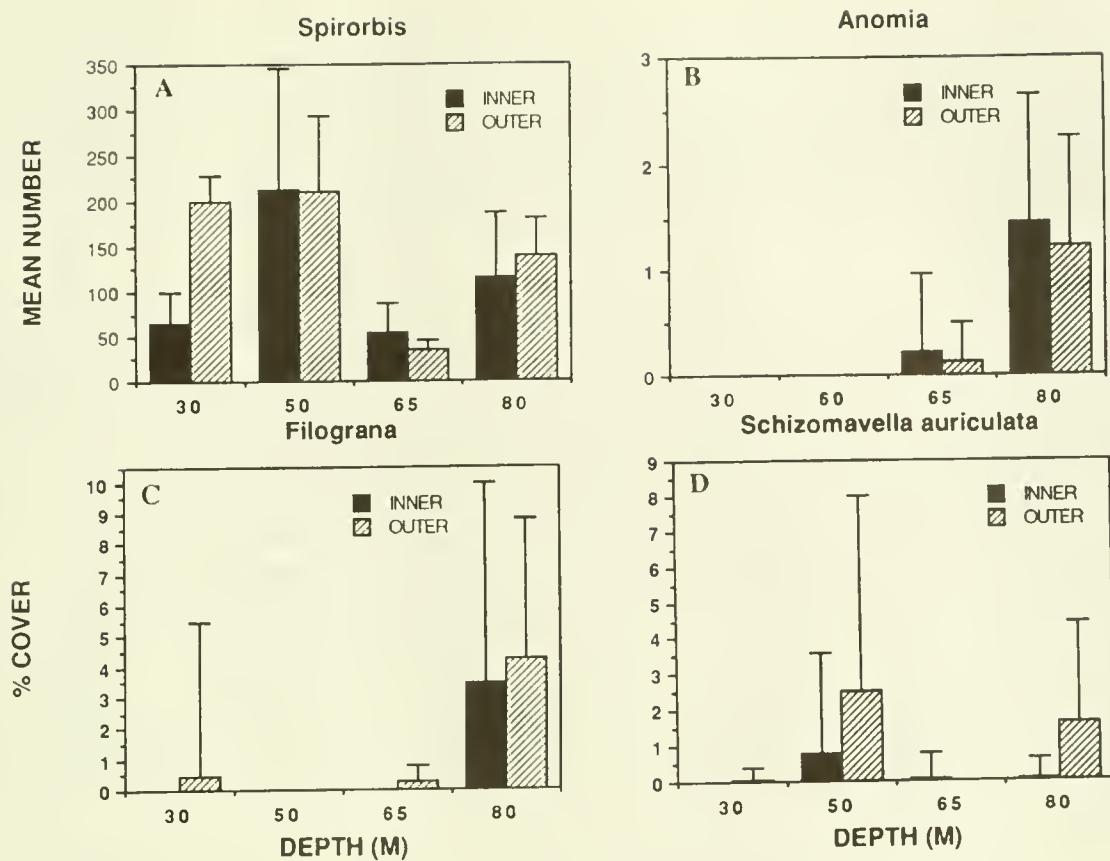


Figure 5.

A. Mean number of Spirorbis at four depths. Mean of 30 m (inner) differs significantly from 30 m (outer), and also from 50 m, (inner and outer), and 80 m (outer) (ANOVA, $p < 0.05$, 7, 33 df, $F = 13.2$) 50 m (inner and outer) also differs from from 65 and 80 m (inner and outer), 30 m (outer) differs from 65 and 80 m (inner and outer), and 65 m (inner and outer) differ from 80 m (inner and outer).

B. Mean numbers of Anomia sp. at four depths. None occur at 30 - 50 m. Means at 65 m (inner and outer) differ significantly from 80 m (inner and outer) (ANOVA, $p < 0.05$, 7, 33 df, $F = 9.4$).

C. Mean percent cover of Filograna implexa at four depths. Means at 80 m (inner and outer) differ significantly from all other means, but not from each other (ANOVA, $p < 0.05$, 7, 33 df, $F = 5.1$).

D. Mean percent cover of Shizomarella auriculata at four depths. Mean at 50 m (outer) differs significantly from all others except 50 m (inner) (ANOVA, $p < 0.05$, 7, 33 df, $F = 3.8$). Mean at 80 m (outer) differs from all others except 50 m (inner and outer).

shallowest depth station (30 m) (Fig. 2). There were very few other encrusting organisms besides the bryozoans. Only three of these organisms covered significant area, the polychaetes Spirorbis spp. and Filograna implexa, and the bivalve Anomia sp.. None of these species accounted for more than five percent cover on any group of plates, but the latter two species were most abundant at the deepest station (80 m) Spirorbis was most common at 50 m (Fig. 5).

Among the erect bryozoans, Idmidronea atlantica was clearly the spatial dominant and appeared to overgrow all other species on the panels including the related species Tubulipora lilliacea which produces more robust but shorter upright processes from a broad encrusting base. Idmidronea grows as a much-branched but loose hemispherical mound (open fan) arising from a small central base. Idmidronea was abundant on the 50 m plates, covering over 50 percent of the plate surface, and covered over 20 percent of the space on panels at 30 and 65 m depth. Harmelin (1973) reports that this species produces a less densely branched colony with less water movement. It was more abundant on inner surfaces (Fig. 2) at all depths, whereas T. lilliacea was most abundant at 30 m and was more abundant on outer surfaces at 30 and 50 m but was equal at 65 m and rare at 80 m. The wholly encrusting Tubulipora flabellaris was of equal abundance on both sides of the 50 m plates and reached less than one percent cover on all others (Fig. 2).

Encrusting bryozoans were most abundant at 30 m where they occupied more than 40 percent of the space, or more than 65 percent if T. lilliacea is considered an encrusting species given its wide encrusting base and short upright branches. Encrusting species were of approximately equal abundance on inner and outer plate surfaces at all depths, but accounted for less than ten percent cover at all depths below 30 m. Since plates from 50 m had so much cover by Idmidronea, there was a negative correlation between this species and the cover of encrusting bryozoans. There was also a strong negative correlation between the abundance of Idmidronea and the abundance of Tubulipora lilliacea at 30-50 m for all plates combined (Fig. 3).

Among the common encrusting species, only Callopora craticula was present in approximately equal abundance at all depths (1-3 % cover). The other common species were generally restricted to a single depth each. Celleporella hyalina covered approximately 20 percent of the surface on the 30 m plates, but was extremely rare at other depths. Porella proboscidea reached three percent cover at this depth and also appeared only as scattered small colonies at deeper stations. Schizomavella auriculata averaged approximately 0.8-2.5 percent cover at 50 m and 1.6 percent on outer plates at 80 m but appeared rarely on all other plates. Lepralia americana was common only at 65 m (outer plates) at 3.2 percent cover and occurred at 0.9 percent cover at 80 m (inner) but was less than 0.1 percent cover on all other plates. Other encrusting species never accounted for more

than a few percent cover on any plates although several of these species also appear to have limited depth maxima (Table 2).

Observations of the two-year settling plates indicate that the low percent cover of encrusting species was maintained at the two deepest stations, but that the two shallower stations achieved 100 percent cover of bryozoans, with the introduction of other phyla including ascidians (Apodium sp.) and crustose coralline algae. The erect bryozoans appear fouled by algae on the 30 m plates and other bryozoans and ascidians were overgrowing both erect and encrusting bryozoan colonies. Similar results were seen on granite blocks. The first year photographs show bryozoan-dominated communities similar to those on settling plates, with Spirorbis, Filograna and a few Anomia. The depth pattern was also similar, with high percent cover at the two shallow stations and low percent cover at the deepest station. The horizontal blocks at 30 m showed greater algal colonization than did vertical settling plates, but the second year's vertical granite slabs showed similar bryozoan dominated assemblages although at lower percent cover. When the second year's granite slab arrays were brought to the surface all mobile species were counted and collected (Table 3) except for those on the 30 m slabs which were left in place and photographed by divers. Of the species found, only Margarites spp., Leptasterias, Henricia and possibly the other gastropods are likely to be bryozoan predators. These species were most abundant at 50 m, corresponding with the highest bryozoan cover.

DISCUSSION

The early successional assemblage in deep rocky habitats of the Gulf of Maine was dominated by approximately twenty species of erect and encrusting bryozoans, two polychaetes, and one bivalve species. The bryozoans occupied well over 95 percent of the available space after one year of colonization, with the other groups rarely accounting for more than one to five percent cover. This preponderance of bryozoans in the assemblage is unique in comparison with other similar studies from shallower temperate communities, although bryozoans form a large fraction of the species in cryptic reef habitats (Buss and Jackson, 1979; Buss, 1980; Jackson, 1977a,b, 1979) and on certain temperate zone subtidal rock walls (Rubin, 1980) and settling plates (Sutherland, 1977; Karlson and Sutherland, 1982). The appearance of ascidians and species from other phyla in the second year of our study indicates that this assemblage will not persist and that community development is likely to continue toward the sponge, ascidian, and sea anemone dominated assemblage typical of unmanipulated rock walls at these depths.

Idmidronea atlantica appears to play a major role in structuring the fouling community at the three shallowest stations, but especially at the 50 m station. This erect species overgrows the only other species with an erect growth form, Tubulipora lilliacea, and many of the other species as well. It

Table 3. Numbers of mobile epifaunal species found on granite colonization blocks (approximately 0.15 m² surface area) after one year at 50, 65, and 80 m depth at Ammen Rock Pinnacle.

SPECIES	DEPTH		
	50	65	80
<i>Henricia sanguinolenta</i>	1	0	0
<i>Leptasterias</i> sp.	11	3	0
<i>Ophiopholis aculeata</i>	13	3	6
<i>Colus stimpsoni</i>	0	0	2
<i>Anachis halinecti</i>	0	4	8
<i>Puncturella noachina</i>	10	0	0
<i>Margarites</i> spp.	25	0	6
gastropod A	2	0	0
<i>Aeolidia papillosa</i>	1	0	0
<i>Harmothoe imbricata</i>	1	0	4
other polychaetes	4	0	2
nermerteans	2	2	18
platyhelminthes	2	0	0
isopods	8	0	22
crinoids (<i>Hathrometra</i>)	0	2	0

covered most space on the inner surfaces of plates at all depths, whereas T. lilliacea covered more space on outer surfaces. Coverage by Idmidronea could be limited either by the availability of larvae in the water column, the rate of water flow, or by events that occur post-settlement, such as interactions with the other species present. The inverse relationship between Idmidronea and all encrusting species combined indicates either that substantial cover of Idmidronea inhibits successful recruitment by the other species or that significant cover of encrusting species inhibits Idmidronea. These hypotheses cannot be separated at present, however, during much of the first year space must have been available to both groups. Idmidronea canopy appears to develop and expand rapidly and could thus have prevented further recruitment or lateral growth of encrusting species. Encrusting species preventing Idmidronea recruitment by precedence would depend on a high percent cover. Even at the 30 m depth, these species reached 40 percent cover only after one year and would thus have been at much lower cover during most of the time period when the panels were invaded by Idmidronea larvae.

Considering the two erect species together, or Idmidronea alone, there is a greater percent cover on inner plate surfaces at all depths. This could result from a more favorable position for settlement, for example in eddies created behind plates. Or it could result from more favorable growth conditions during the year, again because of the particular flow environment on the back surfaces of plates. In 1987 we placed an Interocean S-4 recording current meter 0.4 m off the bottom near the DRS units at each depth. 30 hour records under similar surface wave conditions indicate that the 30 m site received more than twice the water movement of the 65 or 80 m sites and that the 50 m site was intermediate in flow speed. Much of the flow at the shallow sites was wave-generated surge, although there were also periods of strong unidirectional current passing over the top of the pinnacle and lasting for 10 minutes or more. The deeper two sites had little surge but had unidirectional tidally-generated currents that reversed direction as the tide changed. Flow data from September 1987, taken at 0.5 second intervals for one minute of every five minutes, showed a range where most values were 5-25 cm.s^{-1} with peak flows over 50 cm.s^{-1} at 30 m, a range of 2-15 cm.s^{-1} with peaks to 40 cm.s^{-1} at 50 m, a range of 0-12 cm.s^{-1} with peaks to 25 cm.s^{-1} at 65 m and at a range of 0-18 cm.s^{-1} with peaks to 27 cm.s^{-1} 80 m (Fig. 6). Means for the period were approximately 15, 8, 6, and 6 cm.s^{-1} for 30, 50, 65 and 80 m respectively. Water flow alone could, therefore, result in decreased advection of larvae to settling plates at the deeper sites. This does not rule out, however, the possibility that larvae are stratified in the water column and that certain species are thus more likely to settle at any one depth. The depth-specific patterns of many of the bryozoan species indicate that this is very likely. For example, Idmidronea was far more abundant at 65 than at 80 m although flow environments appear similar.

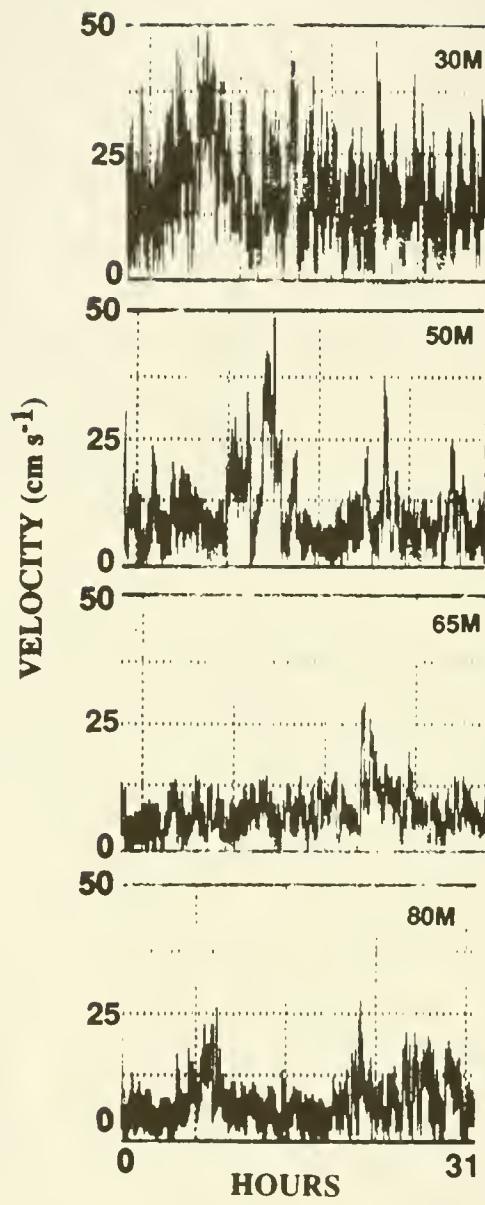


Figure 6.

Short-term measurements of current velocity at four depths on Ammen Rock Pinnacle. Note that current velocity is approximately two-fold higher at the top (30 m) than on the deep flanks (80 m) of the pinnacle.

The InterOcean S4 electromagnetic current meters were programmed to take readings every half second from one minute duration at five minute intervals. Velocity was measured at 40 cm above the bottom.

Other factors that could produce the patterns observed might act after initial recruitment. Differential mortality due to predation, overgrowth competition, or physical disturbance could modify the initial recruitment pattern. Clearly predators are finding the granite blocks and the settling panels. However, there is no indication from our community level predation studies that any of the large invertebrate or fish predators prey on bryozoans as a large part of their diet. The seastar Henricia has been observed feeding on bryozoans as have small Asterias vulgaris and Leptasterias sp. These seastars, and several small gastropods, were common on granite blocks at 50 m and were observed frequently at 30 m as well, although they were not quantified at that depth. They were, however, rare at the deeper two stations. Predation does not appear to be limiting bryozoans to the shallower zones. If anything, predation is more intense at the shallower depths. Competition is also most intense at the 30 and 50 m stations as seen by the lack of bare or unoccluded space at these depths, but is far less frequent at the two deeper stations where much space exists for colonization and lateral growth. Competition must surely be affecting the species composition of the assemblages on the shallower plates. A study of overgrowth competition in this assemblage will be the topic of a later publication on these experiments.

In summary, early community development proceeds more rapidly at the shallower depths (30-50 m) in the rocky subtidal zone of the Gulf of Maine. The early successional assemblage is bryozoan-dominated in the first year, with other phyla becoming common only in the second year of the settling plate experiments. Particular species have distinct depth maxima, and certain species such as Idmidronea show clear patterns of abundance on inner versus outer plates in the array. Predation and competition are likely to be important local structuring processes at the shallower depths, but these may not become important until several years later at the deeper sites (65-80 m) because of lower overall colonization and possibly growth rates of the encrusting species. The first year, and even the second year, assemblages look very different than the communities we observe on undisturbed vertical walls which are dominated by sponges, ascidians, sea anemones, polychaetes, and bryozoans. However, we have seen natural patches on the rock walls that contain assemblages very similar to those on our settling plates. It thus appears that bryozoans are the rapid colonizers in this system and that they colonize and occupy space primarily within the first two or more years, possibly giving way gradually to the more massive species neighboring their originally cleared patch. The importance of bryozoans in this community, and their successional status, would not have been understood without colonization experiments of this type. Analysis of the remaining years' data, and the results from granite substrata, will tell us how closely the settling plates mimic the natural surfaces and will give us more information on the role of benthic predators at this stage of community development.

ACKNOWLEDGEMENTS

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BENTHIC COMMUNITY STRUCTURE AT A SUBTIDAL ROCK PINNACLE IN
THE CENTRAL GULF OF MAINE

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ABSTRACT

Patterns of benthic invertebrate distribution, abundance, and body size were quantified by conducting photo transects from submersibles along a 30-90 m depth gradient, and by SCUBA diving to 30 m at Ammen Rock Pinnacle (ARP) on Cashes Ledge. Three major faunal zones were identified. The shallowest zone is a sparse kelp forest characterized by high densities ($800 \cdot m^{-2}$) of sea anemones, Metridium senile, with abundant encrusting sponges Hymedesmia sp.3 and Halichondria panicea. A striking increase in the abundance of suspension-feeding invertebrates at 38 to 40 m depth marks the beginning of zone 2, comprising mounding sponges, Mycale spp., anemones Urticina crassicornis, and ascidians. The brachiopod Terebratulina septentrionalis is patchily distributed in zone 2, attaining densities $> 500 \cdot m^{-2}$ in some aggregations. A change in the substratum from sloping rock ledge to cobble-gravel bottom at 65 to 68 m is accompanied by a shift in species composition as the cerianthid anemone, Cerianthus borealis, and the polychaete, Myxicola infundibulum, dominate the deepest habitats. The extent to which predation, recruitment, competition and natural mortality can determine patterns of adult epifaunal distribution between and within faunal zones was investigated in controlled field experiments and by photographic monitoring of permanent quadrats and rock walls. We report here on predation and mussel recruitment experiments. The hypothesis that predation by sea stars sets the lower distributional limits of the mussel Modiolus modiolus at ~ 50 m depth was rejected in a one year predator exclusion experiment. Sea star predation may account for the scarcity of Metridium senile at 50 m. The Metridium experiment was inconclusive however, because predator-caused mortality could not be separated from emigration of anemones from the control cages. The lack of mussel spat on plastic filament scrubbing pads set down at 30, 50, 65 and 80 m for one year suggests that deep Modiolus populations are recruitment-limited.

INTRODUCTION

Recent investigations of rocky subtidal communities in the Gulf of Maine have begun to provide us with an understanding of the composition and dynamics of nearshore benthic communities (Sebens 1982, 1985, 1986, Steneck 1982, Logan et al. 1984, Witman 1985, 1987, Vadas et al. 1986), yet little is known about the

ecology of benthic communities in offshore regions. Patterns of community structure have been quantified at only one offshore site, Pigeon Hill on Jeffreys Ledge (Sears and Cooper 1975, Witman et al. 1980, Hulbert et al. 1982, Witman and Cooper 1983). This is surprising considering that offshore rocky ledges in the Gulf of Maine (GOM) support productive fisheries (Bigelow 1917).

The objectives of this report are to provide the first quantitative description of spatial variation in the distribution, abundance and population structure of benthic invertebrates along a 30-90 m depth gradient at a subtidal rock pinnacle in the central Gulf of Maine USA. These data form a necessary community-level baseline for ongoing experimental tests of the processes determining the invertebrate distribution patterns. A later paper will describe temporal variation in community dynamics based on 3 years of photographic monitoring of rock walls at 30, 50, and 65 m depth. The hypothesis that predatory sea stars control the lower depth limit of anemones and horse mussels was tested in a manipulative field experiment conducted at 50 m depth. The alternate hypothesis that the lower depth limit of mussel distribution is determined by recruitment failure was tested by a mussel colonization experiment.

STUDY SITE

Ammen Rock Pinnacle is a submerged rocky peak rising abruptly from 140 m to 28 m depth on the crest of Cashes Ledge approximately 120 km offshore in the Gulf of Maine ($42^{\circ} 51.25'N$: $68^{\circ} 57.11'W$, Fig. 1). Its location far offshore suggests that ARP is partially isolated from the counterclockwise Gulf of Maine gyre (Brooks 1985) that flows along the coast. Because of the steeply sloping bottom topography of Cashes Ledge, the pinnacle site offers an unusual opportunity to study depth variation in epifaunal community structure.

Substratum Type

The range of substrata occurring along the 30-90 m depth gradient is shown in Fig 2. A sloping bedrock shelf composed of peralkaline granite (Toulmin 1957) extends to approximately 65-68 m depth where it ends in a cobble area resembling a talus slope. The topography of the granite ledge is irregular; large expanses of sloping bedrock are interrupted by numerous small joints, resulting in the formation of vertical or undercut rock walls 1-2 m high. Patches of sand and gravel occur between the cobbles and scattered boulders at 68-75 m depth. The bottom beyond 75 m is a sloping sand and gravel plain.

Temperature

Typical vertical profiles comparing temperature at the beginning and end of the summer at ARP are shown in Fig. 3. Comparison of the two profiles indicates that the thermocline is steeper late in the summer than in early summer, due to solar

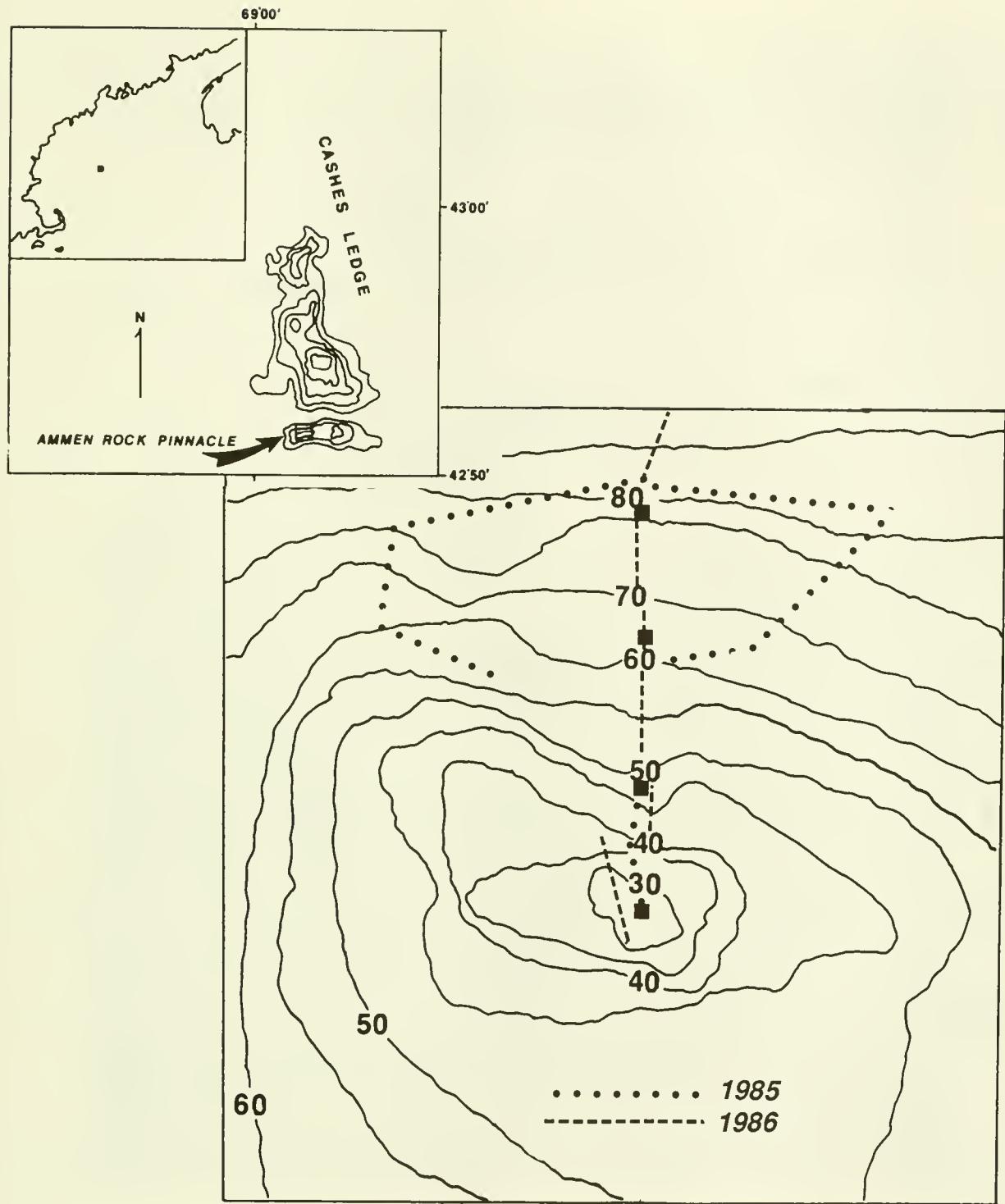


Fig. 1. Location of Ammen Rock Pinnacle on Cashes Ledge approximately 105 km offshore. Inset map at upper left shows location of study site in relation to Cape Cod and Boston. Bathymetric map of Ammen Rock Pinnacle (originally drawn by R. Steneck) from surveys in 1985 and 1986. Black squares indicate location of Depth Specific Research Stations (DRS). Track lines show the location of transects conducted in 1985 and 1986 from the Johnson Sea Link submersible.

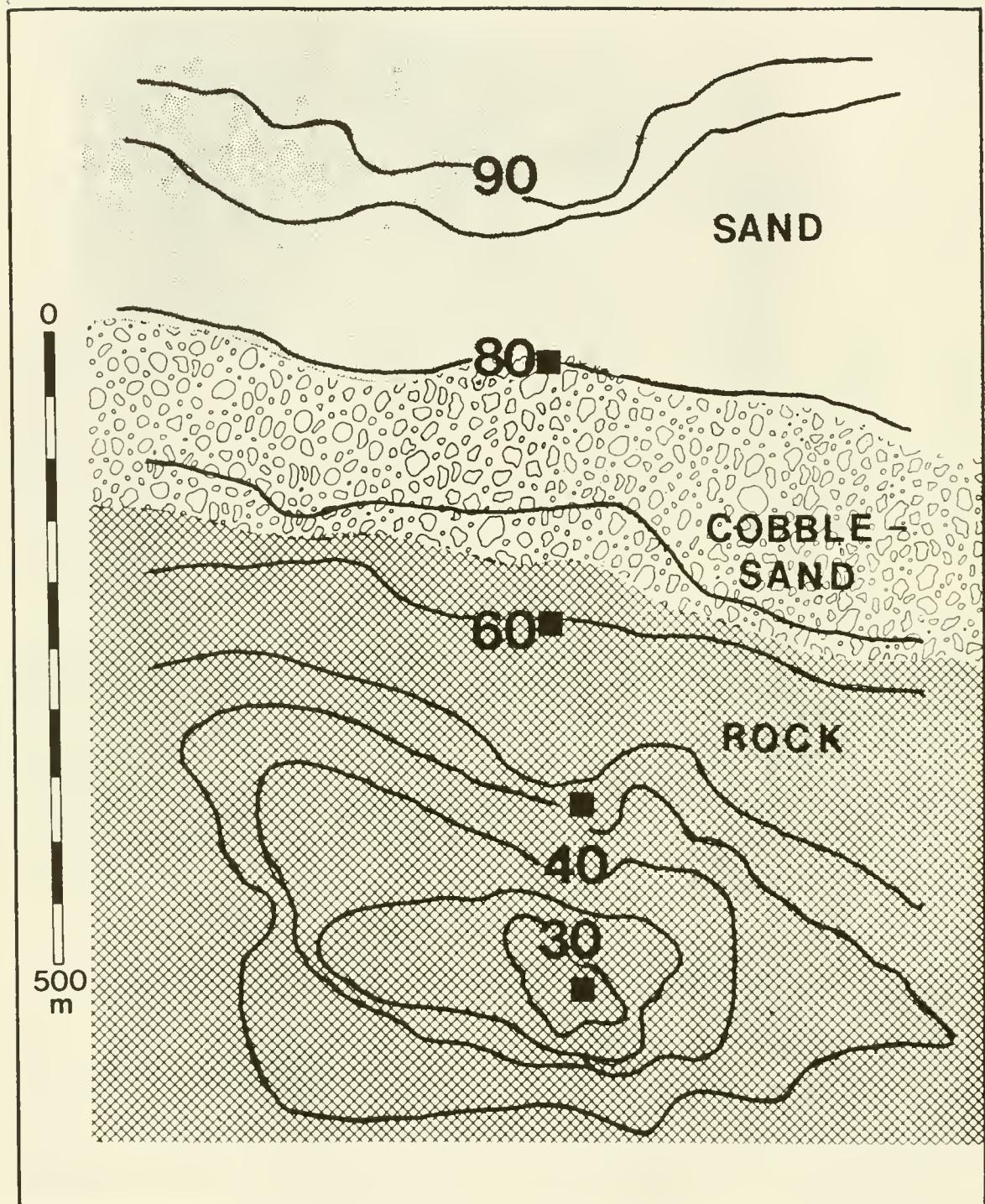


Fig. 2. Map of Ammen Rock Pinnacle showing the range of bottom types along the depth gradient. The sloping granite shelf extends to a depth of approximately 65 - 68 m, where the bottom resembles a talus slope of cobbles and small boulders with patches of sand and gravel. The deep flanks of the pinnacle are a sand and gravel slope.

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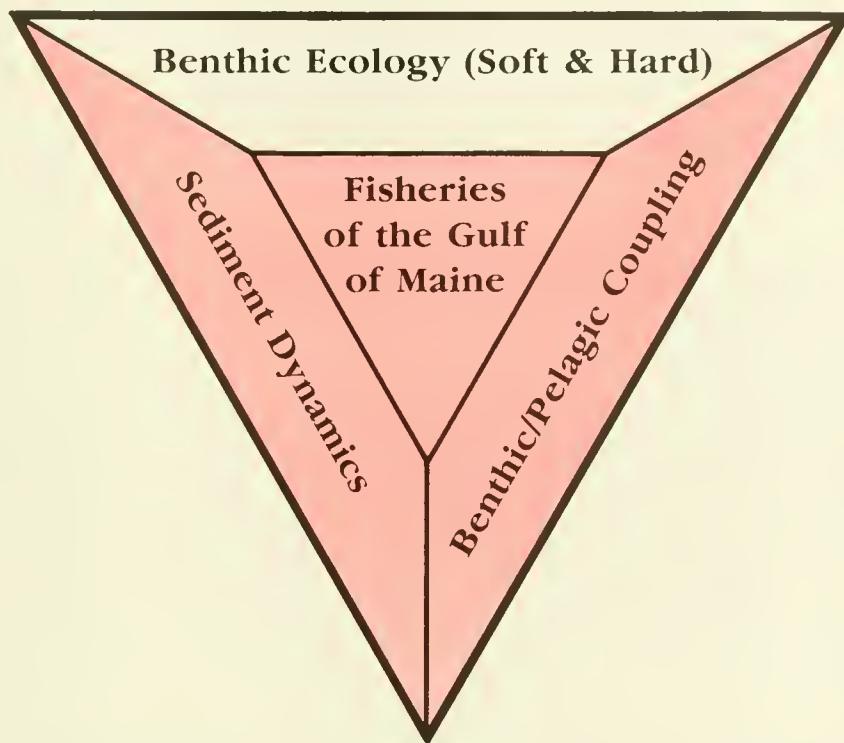
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Benthic Ecology—Soft Substrata



SESSION SUMMARY: BENTHIC ECOLOGY - SOFT SUBSTRATA

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The history of soft bottom benthic studies in the Gulf of Maine has been a long one. The earliest investigations were carried out by fisheries biologists interested in the bottom as a source of food for fishes. All were of a taxonomic nature and essentially came to an end in the late 1880's. In the 1950's and 1960's fisheries scientists again sampled the bottom of the Gulf of Maine, this time as opportunists utilizing surface ships involved in geological studies. With the exception of a single study published in 1975, no studies of the open Gulf benthos were conducted until the 1980's when investigations included both the fishery and more narrowly ecological points of view. The latter have just begun to be published and include biogeochemical as well as biological data. Some of this new emphasis is visible in the four papers making up this section.

Studies of benthic patterns predominate much of the recent work. Macrofaunal patterns, as determined by photographic techniques, are outlined by R. Langton & J. Uzmann, while L. Watling et al. provide an overview of the complex distribution patterns for all benthic species. However, to understand these patterns there is a need for background data on water conditions and food sources. Some of the standard measures, such as total sedimentary organic carbon and nitrogen content, by themselves cannot be used as determinants of sediment nutritional quality. Sampling of the sedimentary regime being fed upon by the suspension feeding sea pens discussed in the chapter by Langton et al., required the development of new technology. See Chapter Four for the method to sample this "fluff" layer, discussed in Mayer et al.

As the following chapters show, benthic studies in the Gulf of Maine have progressed beyond merely sampling for taxonomic studies, though that is clearly still necessary given the number of new taxa being discovered in the deeper areas. The pattern studies reported on here will finally provide the background for the much needed investigations of production and energy flow. Because of the unique resources that it can bring to bear on these problems, I expect that the National Undersea Research Program will continue to play an important role in the studies of the Gulf of Maine benthos.

GENERAL DISTRIBUTION PATTERNS OF MACROBENTHIC
ASSEMBLAGES IN THE GULF OF MAINE

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ABSTRACT

Even though the Gulf of Maine has been investigated since the mid 1800's, there has been published only a single quantitative study of its benthos, and that from a single deep basin. During the years 1982 - 87, a series of quantitative box core samples and qualitative submersible suction samples have been taken from a wide variety of bottom locations throughout the Gulf of Maine. While objective classificatory methods have not yet been used, the faunal distributions observed have been preliminarily subdivided into 7 major assemblages. These assemblages can also be characterized by their sediment and overlying bottom water features.

INTRODUCTION

Investigations of the Gulf of Maine benthos began over 100 years ago with the earliest dredgings of the U.S. Steamers Blake, Albatross, and Fish Hawk. Even so, there still does not exist a comprehensive overview of the benthic assemblages and their distribution patterns. This is due in part to the fact that the bottom of the Gulf of Maine is very heterogeneous, and some areas are not easily sampled. Another factor has been the nature of the sampling. Most often the benthos has been sampled in an opportunistic fashion, taking advantage of cruises planned for other purposes. The study of Rowe et al. (1975) in Wilkinson Basin remains the only published study resulting from a quantitative survey of the benthos in the Gulf of Maine.

The present paper is a summarization of a sampling series taken throughout the Gulf of Maine beginning in 1982. Some of the taxonomic identifications remain to be completed, but already the major patterns are beginning to emerge. Added to the soft bottom data are the results of a set of dive samples taken on rocky ridges and gravel banks through the use of the submersible Delta during the summer of 1987.

METHODS

The 78 soft bottom samples, taken during the summers of 1982-84, were all obtained with a 0.1 m^2 box corer. The sediment was washed over a 500 μm sieve, the residue being preserved in 5% formalin. (A more detailed study of these samples will be published elsewhere.) In July, 1987, a series of 21 dives were made at eleven sites with the submersible Delta on a variety of rocky and gravelly bottoms not previously sampled from surface ships as well as some of the deeper basin sites sampled by box corer. These sites (Table 1) ranged in depth from 240-1050 ft. Samples were collected with a suction pump fitted with a 250 μm bag on one side and a 500 μm bag on the other. Sediment, rock surfaces, and biotic structures were sampled until the bags were full. No effort was made to standardize areas covered nor was it possible to determine how much area had been sampled. On return to the surface, the samples were roughly sorted, with echinoderms being preserved in alcohol and the remainder in 10% buffered formalin.

RESULTS AND DISCUSSION

At the time of writing this preliminary report, 125 species had been identified from the submersible obtained samples. These included 78 polychaetes, 30 crustaceans, and 17 echinoderms (Table 2). While most of the echinoderms were identifiable, the identities of about half the polychaetes still remain in doubt. Among the crustaceans, several of the Amphipoda, and at least one of the Isopoda are new species. The isopod genus, Notoxenoides sp., and the amphipod Lepechinella arctica, are deep-sea taxa that have probably come into the Gulf of Maine with the slope water as it enters through the Northeast Channel. It is likely that many species in the deeper basins will be found to have bathyal affinities as suggested by Rowe et al. (1982).

While these data as well as those collected during the box core survey of the Gulf of Maine need yet to be subjected to classificatory analysis using objective techniques, an underlying pattern in the species distributions has become quite noticeable. At this time it appears there are at least 7 assemblages making up the benthic community of the Gulf of Maine (Figure 1). These assemblages are directly relatable to properties of the overlying water as well as to the composition of the substratum. The assemblages and their characteristics are outlined below.

Table 1. List of dive sites occupied during July 1987 Delta program.

Dive No. UM	General Region	Latitude °N	Longitude °W	Depth (ft)
1	Cashes Ledge	42 51.09	68 58.33	420-480
2	Cashes Basin	42 50.03	69 02.05	600
3	Cashes Basin	42 50.18	69 02.10	605
4	Fippennies Ledge	42 43.87	69 14.97	245
5	Fippennies Ledge	42 43.88	69 15.27	240
6	Fippennies Ledge	42 43.67	69 15.48	260
7	Georges Basin	42 23.46	67 25.87	1055
8	Franklin Basin	42 16.08	67 46.72	760
9	Lindenkohl Basin	42 30.92	67 47.75	760
10	Jordan Basin	43 22.23	67 51.89	810
11	Jordan Basin	43 22.15	67 55.65	820
12	Jordan Basin	43 22.82	67 58.17	820
13	Jordan Basin	43 23.42	68 02.60	760
14	Jordan Basin	43 23.00	68 07.26	700
15	Jordan Basin	43 22.83	68 15.18	593
16	Outer Falls	43 27.52	68 41.06	400
17	Jeffreys Bank, top	43 22.50	68 44.53	290
18	Jeffreys Bank, SW	43 13.07	68 55.05	550
19	Sigsbee Ridge	43 03.46	69 05.87	290
20	Three Dory Ridge	43 13.53	69 19.45	380-412
21	Platts Basin	43 21.25	69 22.49	575

Table 2. Preliminary list of taxa found at dive locations investigated during July 1987 Delta dive program.

Taxonomic Designation	Dive Sites								
	JB	LB	GB	PB	JF	FL	TD	SR	FB
POLYCHAETA									
Dorvilleidae					*				
Dorvilleidae sp.								*	
<i>Schistomeringos caeca</i>							*		
Eunicidae									*
<i>Eunice pennata</i>						*		*	*
Euphrosinidae							*		
<i>Euphrosine</i> sp. 1						*			
Flabelligeridae									*
<i>Brada</i> sp. 1					*				*
<i>Flabelligera</i> sp. 1			*						*
Flabelligeridae sp. 1			*						
Flabelligeridae sp. 2			*						
Flabelligeridae sp. 3							*	*	
Flabelligeridae sp. 4	*								
Flabelligeridae sp. 5	*							*	
Flabelligeridae sp.			*						*
Glyceridae									
Glyceridae sp.				*					
Goniadidae									
<i>Goniada norvegica</i>			*						
Hesionidae						*			
Hesionidae sp.						*			
<i>Neriyama punctata?</i>	*							*	
Lumbrineridae									
<i>Lumbrineris fragilis</i>					*		*	*	*
<i>Lumbrineris hebes</i>	*	*	*	*					*
<i>Lumbrineris impatiens</i>				*					*
<i>Ninoe nigripes</i>				*					*
Maldanidae									
<i>Euclymeninae</i> sp.		*							
<i>Maldane glebifex</i>									*
<i>Maldane</i> sp.			*						
<i>Maldanidae</i> sp.	*		*	*					

Taxonomic Designation

Dive Sites

JB LB GB PB JF FL TD SR FB OF

Nephtyidae

*Nephtys hystricis**Nephtys incisa*

*

Nereidae

Ceratocephale loveni

* *

Nereis zonata

*

*

Onuphidae

Onuphis chonchylega

*

Onuphis opalina

*

Opheliidae

Ophelina abranchiata

* *

*

Ophelina acuminata

*

Orbinidae

Scoloplos fragilis

*

Oweniidae

Galathowenia oculata

*

*

Galathowenia sp.

*

Paraonidae

Aricidea quadrilobata

*

Aricidea suecica

*

Paradoneis lyra

*

*

Phyllodocidae

Phyllodocidae sp.

*

*

Phyllocoete maculata

*

Pilargidae

Ancistrosyllis greenlandica

*

*

*

Polynoidae

Antinoella sarsi?

*

Eunoe nodosa

*

Eunoe spinulosa

*

Polynoidae sp.

*

Taxonomic Designation

Dive Sites

JB LB GB PB JF FL TD SR FB OF

Sabellidae											
<i>Chone</i> ? <i>infundibuliformis</i> ?							*	*	*		
<i>Euchone</i> <i>incolor</i>										*	
<i>Euchone</i> sp. 1							*			*	
<i>Euchone</i> sp.	*	*					*				
<i>Jasmineira</i> sp.									*		
<i>Jasmineira</i> <i>bermudensis</i> ?							*				
<i>Potamilla</i> sp. 1	*		*								
<i>Potamilla</i> sp.			*								
Sabellidae sp. 1		*									
Sabellidae spp.						*			*		*
Scalibregmidae											
<i>Scalibregma</i> <i>inflatum</i>							*				
Serpulidae											
<i>Filograna</i> <i>implexa</i>						*		*	*		
<i>Filograna</i> sp. 1										*	
Sigalionidae											
<i>Neoleanira</i> <i>tetragona</i>	*		*								
<i>Pholoe</i> sp. 1			*								
Sphaerodoridae											
Sphaerodoridae sp.			*								
<i>Sphaerodoropsis</i> <i>minuta</i>										*	
Spionidae											
<i>Prionospio</i> sp.			*		*			*	*		
<i>Prionospio</i> <i>steenstrupi</i>										*	
<i>Scolelepis</i> sp.?							*		*		
<i>Spiophanes</i> <i>kroyeri</i>	*	*								*	
Syllidae											
<i>Autolytus</i> <i>prolifer</i> ?								*			
<i>Exogone</i> <i>hebes</i>						*					
<i>Exogone</i> <i>verugera</i> (<i>profunda</i>)	*						*	*	*	*	*
<i>Sphaerosyllis</i> sp.			*								
<i>Syllis</i> sp. 1										*	
<i>Syllis</i> <i>cornuta</i>							*				
Terebellidae											
<i>Amphitrite</i> ? <i>affinis</i> ?						*					
<i>Polycirrinae</i> sp.							*				
<i>Polycirrus</i> sp.?			*						*		
<i>Streblosoma</i> ? <i>spiralis</i> ?									*		
Terebellinae sp.										*	

Taxonomic Designation

Dive Sites

JB LB GB PB JF FL TD SR FB OF

Trichobranchidae
Terebellides sp.

* * * * *

CRUSTACEA

Amphipoda

Amphilochidae sp. 1

* *

Acantonotozoma rusanovae

Ampelisca sp.

* * *

Dyopedos porrectus

* *

Dulichia falcata

* *

Erichthonius rubricornis

* * *

Erichthonius sp. 1

* *

Eusiridae

* *

Harpinia sp.

* *

Lepechinella arctica

* *

Leucothoidae sp.

* *

Liljeborgiidae sp.

*

Lysianassidae sp.

* *

Oedicerotidae

* *

Pleustidae sp.

* *

Stegocephalidae

* *

Stenothoidae

* *

Unciola n. sp. 1

* *

Isopoda

Desmosomatidae sp.

* *

Eurycopidae sp.

* * *

Janira alta

* *

Munnopsis typica

* *

Notoxenoides sp.

* *

Pleurogonium sp.

* *

Politolana polita

* *

Tanaidacea

Tanaidacea sp.

* * *

Cumacea

Leptostylis sp.

* *

Diastylis cornuta

* *

Diastylis abbreviata

* *

Campylaspis rubicunda

* *

Taxonomic Designation

Dive Sites

JB LB GB PB JF FL TD SR FB OF

ECHINODERMATA

Crinoidea									*	
Asteroidea										
<i>Asterias vulgaris</i>									*	
<i>Ceramaster granularis</i>									*	
<i>Ctenodiscus crispatus</i>	*			*						
<i>Henricia sanguinolenta</i>				*			*	*		
<i>Hippasteria phrygiana</i>					*					
<i>Leptasterias</i> sp.				*				*		
Ophiuroidea										
<i>Amphipholis squamata</i>								*	*	
<i>Amphiura otteri</i>	*									
<i>Ophiacantha bidentata</i>		*		*			*		*	
<i>Ophiopholis aculeata</i>							*	*	*	
<i>Ophioscolex glacialis</i>	*									
<i>Ophiura</i> sp.			*							
<i>Ophiura robusta</i>				*	*			*		
<i>Ophiura sarsi</i>	*			*			*	*	*	
<i>Ophiura signata</i>	*			*						
Echinoidea										
<i>Brisaster fragilis</i>	*									
Total species	33	16	31	19	28	17	25	26	38	17

Key:

JB=Jordan Basin
 GB=Georges Basin
 JF= Jeffreys Bank
 TD=Three Dory Ridge
 FB=Franklin Basin

LB=Lindenkohl Basin
 PB=Platts Basin
 FL=Fippennies Ledge
 SR=Sigsbee Ridge
 OF=Outer Falls

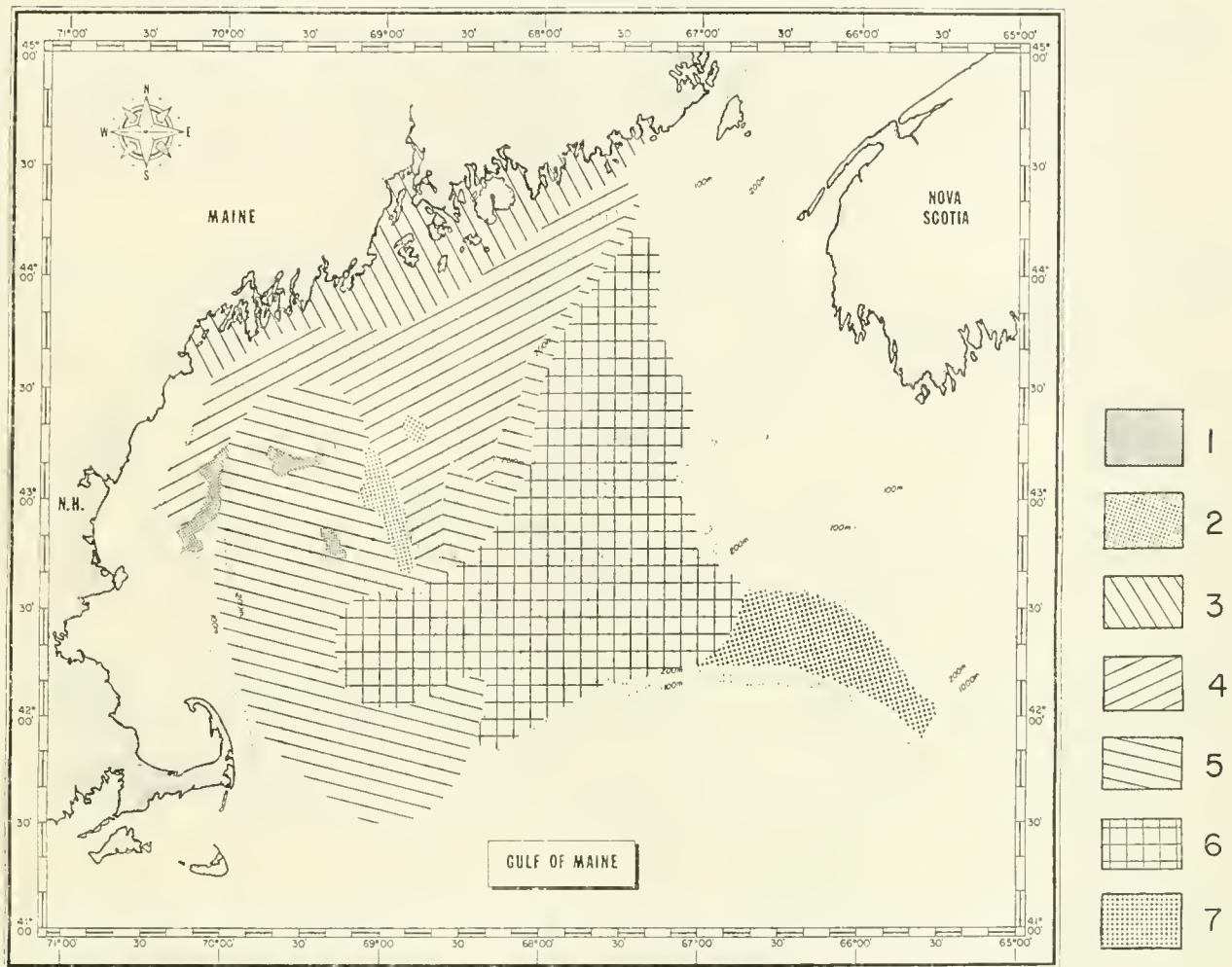


Figure 1. Map of the Gulf of Maine showing the approximate distributions of the 7 major benthic assemblages.

Assemblage 1. Comprises all sandy offshore banks, most prominently Jeffreys Ledge, Fippennies Ledge, and Platts Bank; depth on top of banks about 70 m; substratum usually a coarse sand with some gravel; fauna characteristically sand dwellers with an abundant interstitial component.

Assemblage 2: Comprises the rocky offshore ledges, such as Cashes Ledge, Sigsbee Ridge, and Three Dory Ridge; substratum either rock ridge outcrop or very large boulders, often with a covering of fine sediment; fauna predominantly sponges, tunicates, bryozoans, hydroids, and other solid substratum dwellers; overlying water usually cold Gulf of Maine Intermediate Water.

Assemblage 3: Probably extends all along the coast of the Gulf of Maine in water depths less than 60 m.; bottom waters warm in summer and cold in winter; fauna rich and diverse, primarily polychaetes and crustaceans; probably consists of several (sub-) assemblages due to heterogeneity of substratum and water conditions near shore and at mouths of bays.

Assemblage 4: Extends over the soft bottom well within the depths of the cold Gulf of Maine Intermediate Water, that is, from 60 to 140 m; bottom sediments primarily fine muds; fauna dominated by polychaetes, shrimp, and cerianthids.

Assemblage 5: This a mixed assemblage comprising elements from the cold water fauna as well as a few deeper water species with broader tolerances; overlying water often a mixture of Intermediate Water and Bottom Water, but generally colder than 7°C most of the year; fauna sparse, diversity low, dominated by a few polychaetes, with brittle stars, sea pens, shrimp, and cerianthids also present.

Assemblage 6: Comprises the fauna of the deep basins; bottom sediments generally very fine muds in basins but may have a gravel component in the offshore morainal regions; overlying water usually 7 - 8°C, with little variation; fauna shows some bathyal affinities but densities are not high, dominated by brittle stars and sea pens, and sporadically by a tube-making amphipod.

Assemblage 7: This is the true upper slope fauna that extends into the Northeast Channel; water temperatures are always above 8°C and salinities are at least 35 o/oo; sediments may be either fine muds or a mixture of mud and gravel.

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DISTRIBUTION, ABUNDANCE AND BEHAVIOR OF SEA PENS,
PENNATULA SP. IN THE GULF OF MAINE.

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ABSTRACT

Sea pens, of the genus Pennatula, are major components of the macrobenthic fauna in the Gulf of Maine. In the 1960s the Gulf of Maine was studied as part of a quantitative and qualitative survey of the macrobenthic invertebrate fauna of the east coast of the U.S.A. These data were gathered using traditional benthic sampling gear such as the Smith McIntyre grab, Campbell grab and 0.2 m Van Veen grab. Benthic samples at 62 stations in the Gulf contained sea pens. In the 1980s a macrobenthic study was initiated using a four man submersible system, the Johnson Sea Link, to conduct quantitative photographic surveys with 35 mm still cameras and a video camera and recording system. In 1983-84 these efforts were concentrated in the eastern part of the Gulf including Jordan Basin, Truxton Swell and Georges Basin. In this region pennatulids were ubiquitous but highly variable in density with values ranging from 0 to as high as 8.0/m per still photograph. The greatest numbers occurred in the basins on soft mud bottoms although pennatulids were observed in gravelly substrates on the Swell. In 1985 a dive was made in the western Gulf, in Wilkinson Basin, to complete the distributional survey. In this basin no sea pens were observed over the course of a two and one half hour dive. This suggests that there are fundamental differences in the macrobenthos between the eastern and western Gulf of Maine.

In 1986, the submersible Delta was used to conduct a sea pen behavior experiment on Jeffreys Bank. At the experimental site, four, one-meter square quadrats were deployed and in situ monitoring of sea pen behavior was initiated. Sea pens are capable of retracting into the sediment and the objective of the experiment was to document this behavior for identifiable individuals. The quadrat was visited five times over the next 24 hours. Relatively little change in sea pen behavior was noted. Two sea pens out of seventeen retracted completely.

Two additional dives were conducted in 1985 to collect live animals for potential laboratory observation. Twenty sea pens were set up in the Maine Department of Marine Resources wet lab. Their behavior and survival was monitored. In the lab the animals exhibited similar behavior to that observed in the field. That is, they would extend and contract but on an apparently random basis or, at least, an asynchronous rhythm with regard to other individuals in the tank. The animals survived in the lab for several months and were observed to produce and release gametes in August and September.

INTRODUCTION

In 1983 a macrobenthic survey of the Gulf of Maine was initiated, using the manned submersible Johnson Sea Link, as part of a study of offshore lobster habitat and ecology. During the course of this work it became quite apparent that sea pens, of the genus Pennatula, were one of the more abundant species occurring in, generally, soft bottom areas. A thorough search of published literature on Pennatula resulted in a few accounts of its occurrence and general anatomical descriptions (e.g., Agassiz, 1883; Jungersen, 1904; Kukenthal, 1915; Verrill, 1922; Deichmann, 1936; Bayer, 1956; Bayer et al. 1983). Detailed distributional studies and ecological or experimental work do not, to our knowledge, exist. It is, therefore, the purpose of this paper to; 1) document the extent of Pennatula distribution in the Gulf of Maine and 2) to report on some in situ experimental work aimed at evaluating the sea pens contraction and extension behavior.

METHODS

Starting in the early 1960s, the macrobenthic invertebrate fauna in the Gulf of Maine was studied by the, now, National Marine Fisheries Service as part of a quantitative and qualitative survey of the east coast continental shelf of the U.S.A. Quantitative samples were collected with the Smith McIntyre grab and the Campbell grab, as well as a 0.2m^2 Van Veen grab. Qualitative sampling was done with a 1-meter naturalist dredge, otter trawls and scallop dredges. Samples were fixed in formalin and preserved in alcohol for later taxonomic evaluation. Sea pens were sorted to the ordinal level, Pennatulacea, or in some cases, to the genus Pennatula. Twenty samples, collected between 1955 and 1974, contained 181 specimens which were identified as the species, P. aculeata Danielssen.

In 1983 a series of submersible and remotely operated vehicle operations were initiated in the Gulf of Maine. Although these operations were not all concerned with the study of sea pens, the occurrence of these animals was often observed, thus providing an extensive photographic and videographic record of the presence or absence of sea pens throughout the Gulf.

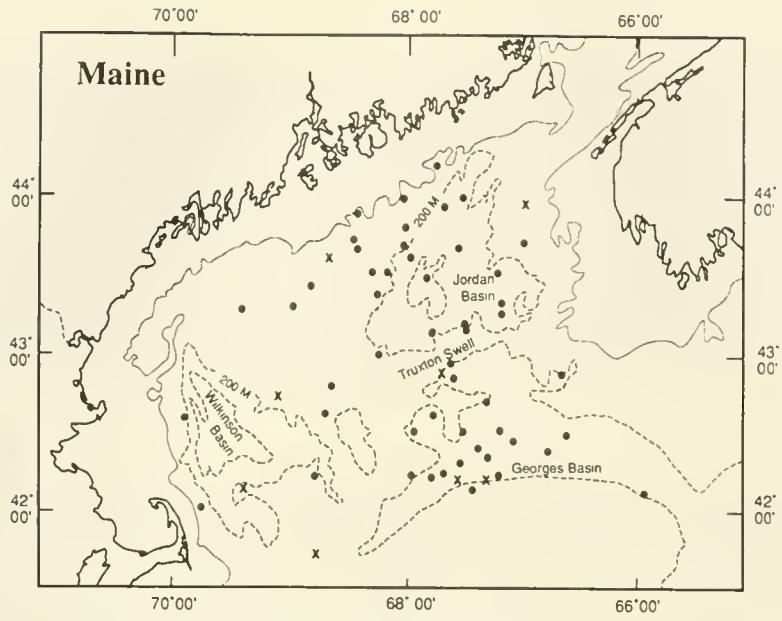
To evaluate the contraction and extension behavior of sea pens an experiment was conducted in 1986 using the submersible Delta. Four 1m^2 quadrats were deployed from the surface ship in an area of relatively high sea pen density on Jeffreys Bank and in situ observations were made on the sea pens inside and immediately outside the quadrats. During a 24 hour period 17 sea pens were monitored in a series of five dives. The presence of sea pens, or absence after the first dive, was noted relative to their position in the quadrats as well as their degree of contraction into the substrate. In other words, individual sea pen behavior was monitored over one 24 hour period.

In addition to the behavior experiment, sea pens were collected for laboratory observation. Animals were scooped up from the bottom with the submersible's manipulator arm, placed in a collecting bag along with their substrate and brought to the surface where they were transferred to a tank of cooled seawater. In the laboratory they were re-established in burrows, made in the substrate collected at the sampling site, and maintained in a refrigerated seawater system. The tanks themselves were darkened and the water renewed every other day.

RESULTS

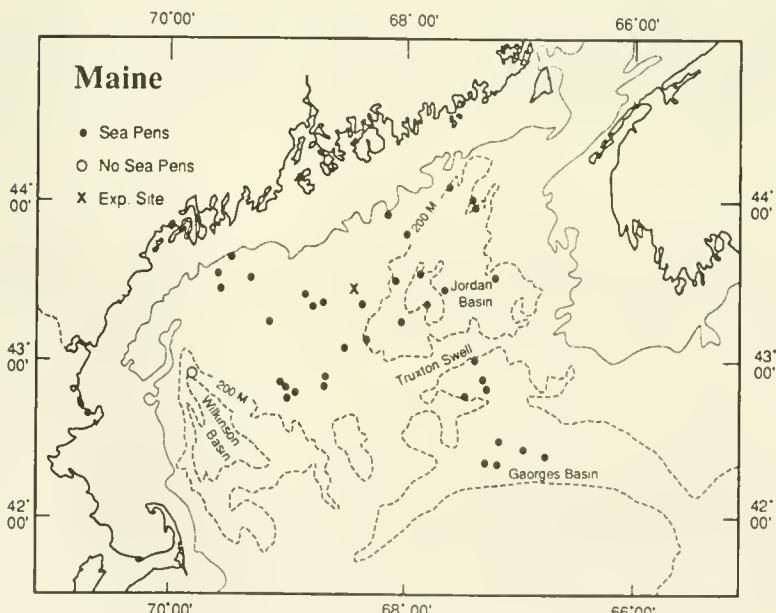
The National Marine Fisheries Service macrobenthic survey sampled 62 stations in the Gulf of Maine region where sea pens of the genus Pennatula were present. Material collected at eleven of these stations were examined in more detail and the species of pennatulid was identified as P. aculeata by Dr. F.M. Bayer. These data are shown in Figure 1. (In the figure the specific level of identification is indicated by an x). Observations on sea pen distribution from submersibles and remotely operated vehicles are shown in Figure 2. In this case, sea pens were simply identified to the generic level, Pennatula, based on photographs, video or direct observations. (The x in this figure denotes the location of the site for behavior studies).

Comparing both plots of sea pen distribution, which cover a time span of 30 years, it is clear that this species has a more or less ubiquitous distribution throughout the Gulf of Maine. A notable absence is in Wilkinson and Murray Basins which are the largest basins in the western Gulf. Neither database includes observations of sea pens in this region, although two stations where only four sea pens were collected fall within the 200 m isobath that includes both Wilkinson and Murray Basins as well as three other smaller basins in the western Gulf. In fact, one submersible dive in 1985 was conducted in the deepest part of Wilkinson Basin ($42^{\circ}45.21'N$ $69^{\circ}49.48'W$) specifically searching for sea pens. A two and one half hour transect produced no sightings. In 1987, remotely operated vehicle operations on the western side of Wilkinson Basin also resulted in no sea pen sightings, although these dives were not specifically searching for Pennatula.



Gulf of Maine - Sea Pen Distribution
N. M. F. S. Benthic Database

Figure 1. Distribution of sea pens of the genus *Pennatula*, in the Gulf of Maine from macrobenthic surveys conducted by the National Marine Fisheries Service between the years 1955 to 1974. Location of animals identified to species, *P. aculeata*, are noted in the figure with an X.



Gulf of Maine - Sea Pen Distribution
Submersible and ROV observations

Figure 2. Distribution of sea pens, of the genus *Pennatula*, in the Gulf of Maine from manned submersible and remotely operated vehicle dives between the years 1983 through 1987. In this figure the x marks the location of an *in situ* sea pen behavior experiment conducted in 1986. The open circle denotes the dive location in Wilkinson Basin where no sea pens were observed over the course of a two hour dive.

Sediment samples were collected as part of the macrobenthic survey and on some of the submersible dives. The distribution of Pennatula was compared to sediment types and found to occur over a broad range of grain sizes. It was most abundant in silts and clays but on occasion was found in gravelly areas.

The microscale distribution of sea pens is shown in relation to the course of the Johnson Sea Link submersible dive #1414 in Figure 3. This dive was conducted in Georges Basin ($42^{\circ}28.18'N$ $67^{\circ}20.06'W$), at a depth of 1060 feet, and represents the highest density of sea pens observed in the Gulf of Maine. The photo frame numbers represent 200 random photographs taken during the dive transect. The density of sea pens varied substantially during the course of the dive with several clusters of sea pens being evident, as well as a reduction in density along the dive transect. Another way of examining this data is to plot the numbers of photographs containing the different numbers of sea pens (Figure 4). From this plot, it is evident that up to 55 sea pens occurred in a single frame. Chi-square analysis of these data was utilized to compare the actual distribution with that of a calculated Poisson distribution. The data did not fit the Poisson or random distribution. Subsequently, a negative binomial, which is often successfully used to describe contagious invertebrate distributions (Elliot, 1983), was fit to the data. Again, no significant fit was found between the observed and expected values. No other mathematical models have been fit to the dataset since, as described below, the actual observed microscale distribution may be modified by individual sea pen behavior which, in turn, may negate simple mathematical modelling of the population's distribution.

Bearing in mind that sea pens can, and do, occasionally retract completely into the sediment, the observed numbers of sea pens per photograph represent an average density for dive #1414 of 2.5 m^{-2} with values ranging from 0 to over 8 m^{-2} per individual photo frame. In another area of Georges Basin average density dropped to 0.19 m^{-2} while in other regions of the Gulf, such as Truxton Swell and Jeffreys Bank, density averaged 0.2 m^{-2} and 1.4 m^{-2} , respectively.

Sea pen behavior was observed in and around four 1m^2 quadrats at a station on Jeffreys Bank in 1986. A total of 17 sea pens were monitored over one entire 24 hour period (9 inside the quadrats and 8 outside) to evaluate their extension and contraction behavior. Only two sea pens were observed to contract completely; they were no longer present during the final dive. One other sea pen was noted to appear from a fully contracted position between the second and third dive. This was also one of the two sea pens that contracted completely, again, during the last dive. All other sea pens maintained a fully extended posture over the course of the experiment.

In the laboratory, animals collected from Jeffreys Bank, established themselves in burrows and exhibited extension and

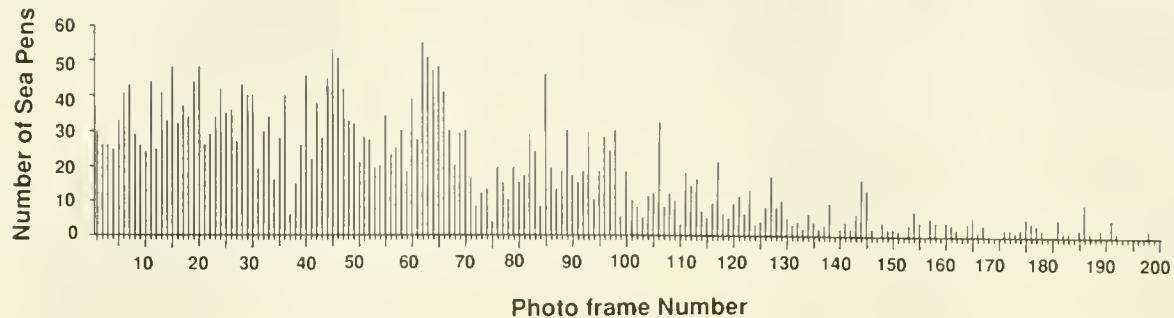


Figure 3. Distribution of sea pens along a submersible dive transect in Georges Basin. The x- axis represents the photo frame number for a series of 200 random 35 mm color photographs taken over the dive. The y-axis is the number of sea pens per photograph. Note the reduction in total numbers of sea pens over the course of the dive as well as variation from photograph to photograph. The area of sea floor per photograph is approximately 6.7 m^2 .

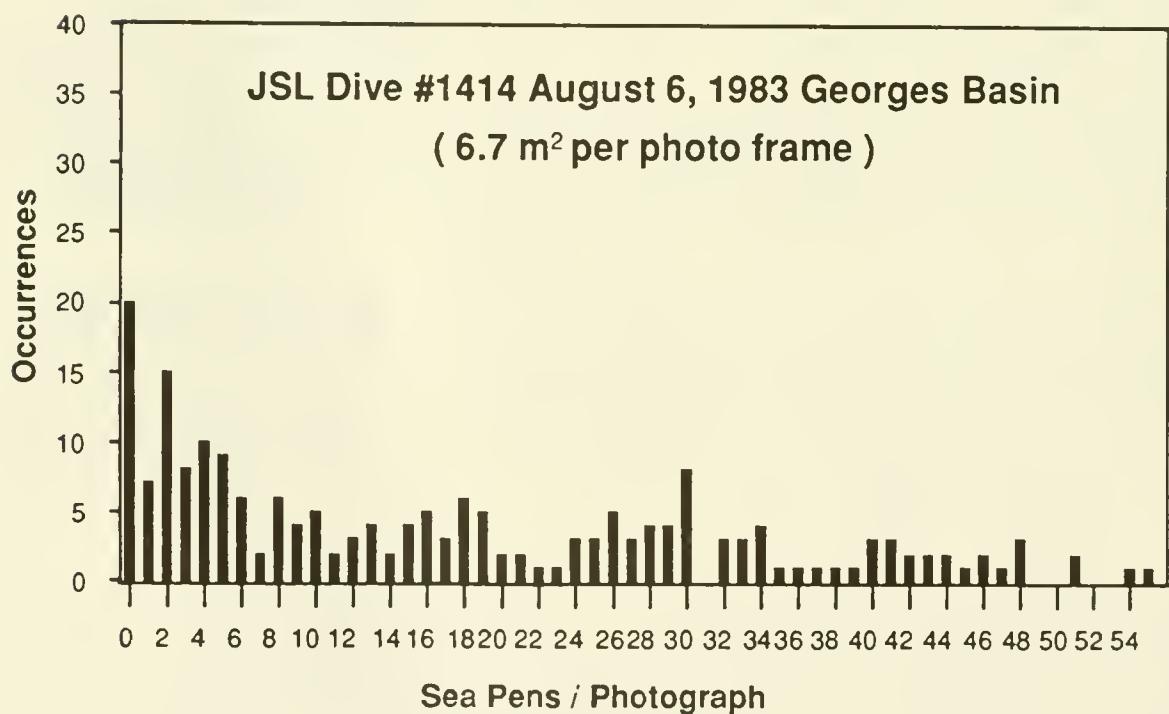


Figure 4. Frequency distribution plot of the numbers of sea pens per photograph for the same submersible dive shown in figure 3.

contraction behavior. Results are purely qualitative, since the laboratory conditions were not optimal, but the sea pens were observed to retract completely into the sediment and reappear on a random or, at least, asynchronous rhythm with regard to other individuals in the tank. The animals survived several months in the laboratory and were observed to release gametes in August and September. After this, the condition of the animals deteriorated markedly. Attempts were made to feed the sea pens both zooplankton and algal cultures but no feeding response was observed.

DISCUSSION

Two species of sea pen of the genus Pennatula (i.e., P. aculeata and P. grandis = P. borealis) are reported to occur along the north Atlantic coast from the Davis Straits to Chesapeake Bay (Deichmann, 1936). They occur in deeper waters, usually greater than 60 fathoms (Miner, 1950). Although relatively common in the Gulf of Maine, the details of their distribution have not previously been examined (Figure 1 and 2). In fact, the magnitude of their abundance was not fully appreciated until the submersible based macrobenthic surveys began in 1983. Pennatula is reasonably ubiquitous in the Gulf, with the exception of Wilkinson Basin. Submersible dives in this basin, with the specific objective of searching for sea pens, found no animals. The one previous submersible study in Wilkinson Basin (Rowe et al., 1975) also did not include Pennatula in the faunal list. The apparent absence of this species from Wilkinson Basin raises a fundamental question about environmental conditions in the basins of eastern (Jordan and Georges) and western (Wilkinson) Gulf of Maine. The pattern of water circulation, originally described by Bigelow in 1927, has recently received much attention (e.g., Hopkins and Garfield, 1979; Brooks, 1985, 1987, Ramp et al., 1985) and this may well be the ecologically controlling factor. However, the link between the physical environment and faunal characteristics in the basins has yet to be examined.

Accurate estimates of sea pen density are confounded by the behavior of this group of animals. These otherwise sessile invertebrates are capable of retracting completely into the sediment thus avoiding predators as well as visual or photographic counts. Contraction and extension behavior is well documented for shallow water species (Birkeland, 1974; Buisson, 1964, 1980; Dickson, 1978; Hoare and Wilson, 1977; Imafuku, 1976, 1980; Magnus, 1966; Mori 1944a, & b, 1945, 1947a & b, 1949, 1950, 1960; Pavans de Cecatty and Buisson, 1965; Pavans de Cecatty et al., 1963) but no data are available on deeper water forms like Pennatula. Results reported here confirm that deeper water animals show a similar behavior. Further study is needed to understand when and why the animals contract before we can accurately estimate density. In shallow water, pennatulids appear to expand to feed on a diel cycle in response to light or increases in zooplankton. In deep water, light is greatly reduced or totally absent so this cannot serve as a cue for extension and contraction. The population observed over one

twenty-four hour cycle showed no obvious coordinated rhythm; longer observational studies are needed to examine animal behavior. One other difference between shallow and deep water pennatulids is the rapidity with which they contract. On several submersible dives, sea pens were either hit gently with the submersible's arm or observed to be hit by a crab scurrying out of the sub's path. In both instances the sea pens showed no immediate response. Only after persistent prodding with the arm did one animal sluggishly, and only partially retract. Such behavior is obviously of little value as a defense mechanism suggesting that, perhaps, deep water sea pens are cued by internal, physiological needs rather than external stimuli.

The behavior of Pennatula also confounds a detailed evaluation of the microscale distribution of the animals (Figures 3 and 4). The photographic, distributional data collected on a single submersible dive, in the area of apparent highest sea pen density in the Gulf, could not be described by either a Poisson or negative binomial distribution. Although it is not possible to know with any confidence, it may be that the contraction-extension behavior biases these distributional patterns. In any event, if a mathematical model were found to fit the data in Figure 4, the biological meaning is suspect without a better understanding of sea pen behavior.

ACKNOWLEDGEMENTS

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A SURVEY OF THE MACROBENTHOS IN THE GULF OF MAINE
USING MANNED SUBMERSIBLES

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ABSTRACT

During the summers of 1983 through 1985 the Johnson Sea Link manned submersible systems were utilized to survey the macrobenthic fauna in the Gulf of Maine. Quantitative 35 mm color photographs were taken at 29 stations and 5714 photos were analyzed. A total of 47 catagories of macrobenthic organisms were routinely identified in the photographs. Eighteen taxa represented 96% of all the organisms counted, and of these 18 only five groups, from two phyla, were dominant. Ophiuroids and asteroid starfish were the dominant echinoderms while cerianthid anemones, pannatulids and Bolocera anemones were the dominant cnidarians. The relationship between sediment type and the macrobenthos was also investigated. Again, relatively few species groups were numerically important and these groups showed a reasonable level of substrate specificity. Pennatulids occurred on a variety of substrates but were most abundant on clayey-silt. Cerianthid anemones were found in sandy substrates while Bolocera dominated in gravel. Pandalid shrimp occurred on sandy-silt while scallops were generally restricted to sand. Asteroid starfish covered a range of coarser substrates and ophiuroids were dominant on silts and clays. The only fish observed in any quantity were silver hake and these were often seen resting on the bottom on silty-sand and finer sediments.

INTRODUCTION

The Gulf of Maine has been described as an epicontinental sea or macroestuary extending from Massachusetts to Nova Scotia (Uchupi 1965, 1966; Emery and Uchupi 1972; Campbell 1986). It has its origins in the last glacial period, 11,000 BP, having been shaped by both fluvial and glacial erosion (Emery et al. 1965; Ziegler et al. 1965). The resulting uneven topography and mixture of sediments offer a variety of habitats for the establishment of benthic organisms, of both commercial and noncommercial value (Rich 1929; Emery et al. 1965). The distribution and abundance of commercial species have been studied over the years (e.g., Bigelow and Schroeder 1939, 1953)

but with few exceptions, primarily small scale studies, the benthic communities have received little attention (e.g., Dexter 1944; Stickney 1959; Hanks 1964; Sears and Cooper 1978; Larsen 1979; Larsen et al. 1983a, b; Hulbert et al. 1982; Witman and Cooper 1983). Published reports describing the soft bottom benthos in the offshore regions of the Gulf are limited to the work of Emery et al. (1965), who conducted a geological and biological survey of the U.S. east coast continental shelf, and a study of two deep basins in the Gulf, Wilkinson and Murray, by Rowe et al. (1975). Several, as yet unpublished, databases also exist describing the Gulf's benthic communities. One of these is a detailed expansion of the work outlined by Emery et al. (1965) (Theroux and Wigley, pers. comm.) while the other is from recent box core sampling in the Gulf (Watling, pers. comm.).

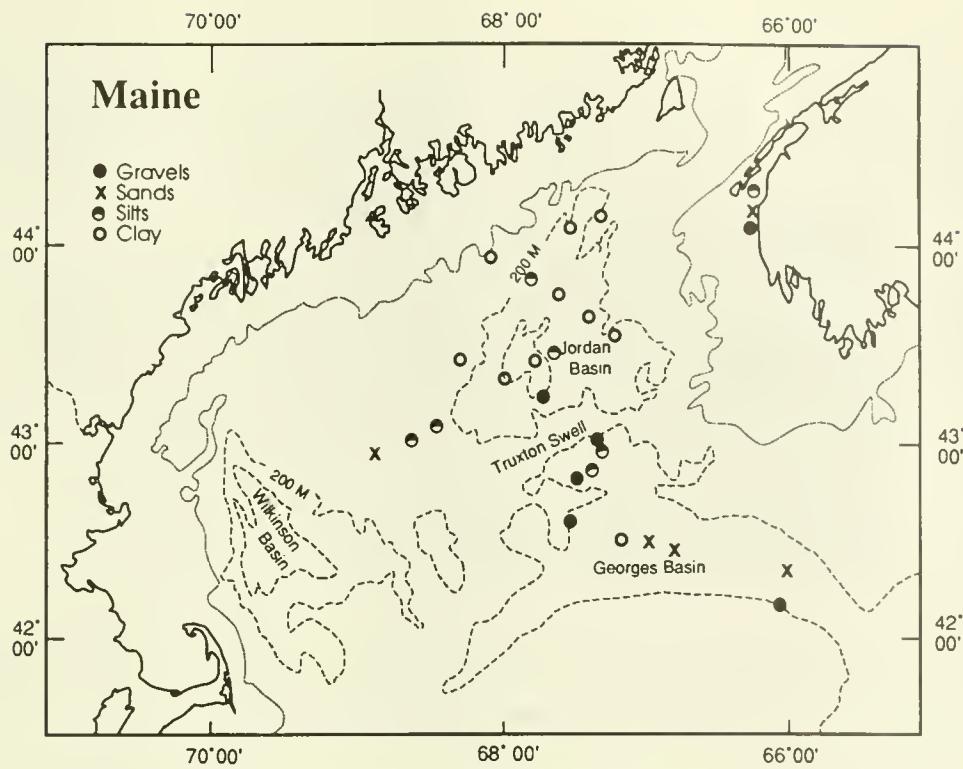
The current study was initiated as a submersible based survey of offshore lobster habitat in the Gulf of Maine. In addition to this fisheries orientation, however, numerous 35 mm color photographs were taken to characterize the associated macrobenthic fauna. In light of the paucity of information on the Gulf's macrobenthic communities, it is the purpose of this paper to summarize the photographic data collected from the years 1983 through 1985 using the Johnson Sea Link submersible systems.

METHODS

During the summer of 1983 through 1985 the Johnson Sea Link manned submersible systems were utilized to survey the macrobenthic fauna at 29 stations in the Gulf of Maine. The purpose of the study was to document offshore lobster habitat, therefore, dive site selection (Figure 1) was based on information on the commercial trap fishery as well as National Marine Fisheries Service data on lobster catches in their biannual groundfish trawl surveys. Submersible dives at each station followed a standard procedure, with the scientist recording observations on a cassette tape or video camera as well as collecting surficial sediment samples over the course of a transect. In addition to these data, 35 mm color photographs were automatically taken at 10 to 15 second intervals throughout the dive. In the laboratory a minimum of 200 randomly chosen photographs from each dive, or all photos taken during the entire dive if less than 200 frames total, were individually examined and the macrobenthic animals identified and enumerated. Forty seven categories of macrobenthos representing a variety of taxonomic levels were identified including twenty seven invertebrate groups and eighteen species of fish.

RESULTS

Sampling sites are shown in Figure 1. The stations were visited during the summer months over a three year period, 1983 through 1985. In 1983, locations in the outer, Georges Basin, and northward towards Truxton Swell were sampled while in 1984 the stations in the middle of the Gulf and Jordan Basin were



Macrobenthic Sampling Sites 1983-1985
JOHNSON SEA-LINK Submersibles

Figure 1. Dive site locations for 29 dives constituting the macrobenthic survey, 1983-1985 using the JOHNSON-SEA-LINK submersible systems.

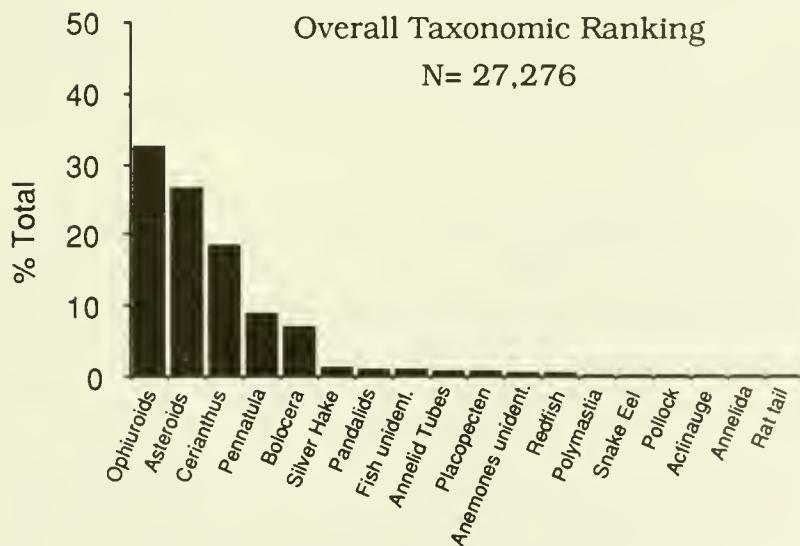


Figure 2. Overall taxonomic ranking, expressed as % of the total number of organisms observed (N=27,276), for 29 submersible dives in the Gulf of Maine from 1983 through 1985.

visited. In 1985, a series of stations running from the center of Jordan Basin to the northeast towards the Bay of Fundy were to be sampled. Unfortunately, weather limited the available dive time and forced diving operations inshore toward the Nova Scotian coast after only three stations were sampled.

Sediment types are also shown in Figure 1. From one to seven sediment samples were collected to characterize each site for surficial grain size. The analyses were done by the U.S. Geological Survey. The general sediment pattern, as shown in the figure, is a gradation of coarse to fine sediments. Georges Basin is, generally, sandy along its midsection changing into a gravelly area towards the swell. Jordan Basin, which is north of Georges Basin, is dominated by the finer silts and clays.

In total, 5714 color photographs (35mm slides) were examined from the 29 submersible dives. Over twenty seven thousand individual organisms were counted. The overall taxonomic ranking is shown in Figure 2, based on percentage of the total numbers observed, for the top 18 taxonomically distinct groups. These 18 groups represent 96% of all the organisms counted. From the figure, it is clear that there are only five dominant taxa representing two phyla, the Echinodermata and the Cnidaria. Ophiuroids and asteroid starfish are the dominant echinoderms while mud burrowing anemones, sea pens and rock anemones account for the dominant cnidarians.

If the same data are examined on a year by year basis there are, again, very few dominant groups. In addition to the echinoderms and cnidarians, arthropods (pandalid shrimp) were reasonably abundant in 1984 while annelid tubes occurred at the stations visited in 1985 (Table 1). The year by year breakdown, like the overall ranking, demonstrated a very simple picture for the softer sediment macrobenthic communities in the Gulf of Maine. Seven taxonomically distinct groups accounted for 97 to 99% of all the biota observed.

The relation between sediment type and animal abundance is shown in Figure 3. For this figure the data were summarized, on a % number basis, for each substrate type. Any taxonomic group that accounted for $> 5\%$ of all observations for any one sediment type were included. As shown previously, relatively few taxa dominate; only 8 groups accounted for 95% of the observations in this substrate specific breakdown of the database. What is of interest is the substrate specificity of the various groups. Sea pens, of the genus Pennatula, occur in gravel to clayey-silt, for example. They are, however, more common in clayey-silt than gravel; occurring at only one gravelly station compared to ten stations dominated by clayey-silt. Cerianthus, the mud burrowing anemone is also not especially substrate specific. It was found over the entire gradation of sandy substrates. Bolocera on the other hand, is an anemone that attaches to hard, rocky, substrates. Consequently, it was observed only in areas of gravel and sand.

	Bouldery-Gravel	Gravel	Sandy- Gravel	Sand	Sandy-Silty-Gravel	Sandy-Silt	Silty-Sand	Sand-Silt-Clay	Clayey-Silt-Sand	Clayey-Silt
<i>Pennatula</i>	15		5	11					56	
<i>Cerianthus</i>		63		72	9	37	2			<1
<i>Bolocera</i>		54	12							
<i>Pandalids</i>				<1	5					<1
<i>Placopecten</i>			5							<1
<i>Asteroids</i>	89	26	35	73	<1	3	36	1		
<i>Ophiuroids</i>					20	70		95	97	40
<i>Silver Hake</i>							8	1		<1

Figure 3. Occurrence of dominant macrobenthic groups broken out by substrate type. Any taxon that accounted for $\geq 5\%$ of all organisms counted in any of the substrate categories was included in the figure.

GROUPS	% of Major Groups by Year		
	1983	1984	1985
<i>Pennatula</i>	38.0	28.0	4.0
<i>Cerianthus</i>	38.3	5.0	10.3
<i>Bolocera</i>	10.1	--	1.3
<i>Annelida</i> (tubes)	--	--	2.1
<i>Pandalids</i>	--	1.2	—
<i>Asteroids</i>	6.5	2.5	11.5
<i>Ophiuroids</i>	2.8	62.2	67.9
TOTAL %	97.5	98.9	97.1

Table 1. Breakdown of the major groups of benthic organisms, expressed as % number of total organisms observed, for each of the three years of the survey. These seven groups account for 97 to 99 % of all macrobenthic animals observed in any given year.

On the sandy substrate these anemones were often observed attached to a rock outcrop or loose boulder rather than directly on the sand itself. Pandalid shrimp were found on sandy-silt while the sea scallop, Placopecten, was primarily restricted to sand. The asteroid starfish which include a variety of genera and species (e.g., Asterias, Hippasteria, Henricia, Crossaster, Solaster) occur over a broad range of substrate types. They are, however, more prevalent on the coarser grained substrates and virtually absent on clay. In contrast, ophiuroids do not occur on gravel substrates in any numbers while they are the dominant species group on silts and clays. The only fish species that occurred in sufficient numbers to demonstrate any substrate specificity was the silver hake Merluccius bilinearis. This species was observed resting on the bottom on silty sand and finer sediments.

DISCUSSION

This study is the first, broadscale, macrobenthic survey in the Gulf of Maine using manned submersibles. The characterization of the benthos that emerges from this work is surprisingly simple. Relatively few taxa, or taxonomic groups, from two phyla dominate the benthos on a numerical basis (Table 1, Figure 2). It's interesting that these phyla (Echinodermata and Cnidaria) are different from the dominants found by Emery et al. (1965), (Arthropoda and Annelida) in their survey using surface deployed sampling gear. Obviously both temporal and spatial scales can account for some of these differences; Emery's stations extended well beyond the confines of the Gulf of Maine and predates the present work by twenty years (compare Figure 1 with Emery et al's. Figure 3). In a more detailed evaluation of the same database Theroux and Wigley (MS, in prep.) found that in the Gulf of Maine, per se, molluscs, annelids and crustaceans were the three numerically dominant groups. Echinoderms were fourth in abundance with ophiuroids accounting for the majority of this group. Again, the differences between the studies, even with reduced spatial variability, is substantial. It is unlikely, however, that climatological changes over twenty years would account for these differences. It is more likely sampling methodology, quantitative grabs vs photographs, generated the differences. Grab sampling would be expected to produce samples containing higher numbers of molluscs and annelids whereas photographs highlight the epibenthic organisms. One might expect more overlap between the two databases with groups like the crustaceans but, again, the sampling methodology virtually precludes this. Theroux and Wigley reported crustaceans as being the third most dominant group of animals but these were almost exclusively amphipods which can not be resolved in the submersibles photographs. As a consequence of the sampling methods, it is truly impossible to quantitatively compare the two databases. What is needed is simultaneous sampling using the submersible to characterize the macro-epibenthos and general habitat and grabs to quantify the infauna.

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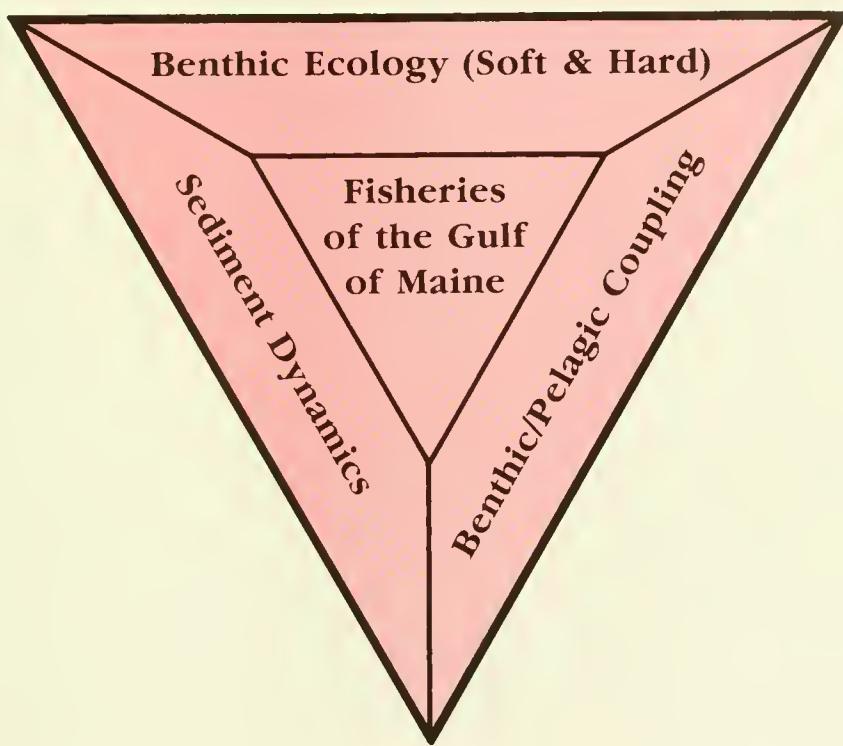
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Gulf of Maine Sediment Dynamics



SESSION SUMMARY:
GULF OF MAINE SEDIMENT DYNAMICS

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As part of the overall ecosystem of the Gulf of Maine, sediment dynamics is a critical area of study. Sediments are an important part of the benthic substrate, controlling distribution of organisms to a large degree, and are intimately involved in the food web through transport pathways, substrates for microorganisms, and through storage and recycling of nutrients within the bottom. Besides nutrients, sedimentary particles also transport, store and recycle pollutants, affecting the benthos in less beneficial ways.

A prime area of current research is the source, transport pathways, and sinks of sedimentary particles. Part of that study is the present distribution of sediment types and the geologic record of past distributions. It is probable that sediments are segregated into deep channels by tide and wave scour, and the action of slumps and turbidity currents. It is clear that there is no simple blanket produced by hemipelagic settling. The redistribution of sediments by slumps, tidal currents and wave action occurs at least seasonally, and probably at a more frequent rate on most ridges and shoals. The rate at which this material is carried to deeper basins has important consequences to benthic communities. On hard bottoms, being swept clear of sediments has a distinct advantage. On muddy bottoms, input of new sediments is advantageous up to a certain rate, since new food is made available. When sediment smothers the bottom to a critical depth, however, macroinvertebrates will be killed, and nutrients will be buried too deeply for excavation. The rate of sediment accumulation and the episodicity of processes thus requires quantification.

Three major nearshore environments have been identified in the Gulf of Maine: rocky ledge, sandy nearshore ramp, and basin. Rocky ledges are swept clear of sediments, but often have a talus pile of angular rocks at their base. Next to the talus pile are carbonate shell hash-rich gravel aprons, grading into basinal muds or sand. Sandy ramps are reworked paleodeltas or beach shoreface deposits. Sand waves and oscillation megaripples provide evidence for current and wave activity on these surfaces. Basins are usually the sites of former estuaries, produced at the early Holocene low sea stand, and are muddy and abundantly bioturbated.

Not all the sediment found within the system is mineral particles; a large percentage is organic, either as fecal pellets composed of plankton which have passed through the gut of larger organisms, or films and coatings of mucus and bacteria. The composition and methods of breakdown and utilization of this material at the base of the food web are critical issues for the overall productivity of the Gulf of Maine. Buried organic-rich sediment has produced natural gas accumulations visible in seismic reflection profiles and possibly as seeps in pockmarks on the seafloor. These phenomena are important clues to the location and nature of past nearshore and estuarine environments.

Studies of the sediment-water interface, the interaction of benthic communities with the sediments, and the rate and nature of sediment transport are all addressed within this report. In the following paper, Belknap, Kelley and Robbins report specifically on the complex mosaic of sediment types, which reflects both relict distributions and modern sedimentary processes, and suggest linkages to other benthic oceanographic studies.

SEDIMENT DYNAMICS OF THE NEARSHORE GULF OF MAINE:
SUBMERSIBLE EXPERIMENTATION AND REMOTE SENSING

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ABSTRACT

Observations during submersible dives covering more than thirty linear kilometers of sea-floor have been integrated with seismic reflection profiling, side-scan sonar survey, and grab samples to produce a preliminary model of sedimentary processes on the Maine inner continental shelf. Sediments occur in a complex mosaic which is a composite of sedimentary materials inherited from glacial-deglacial, shoreline, and fluvial environments, and overprinted by modern marine systems (thus, a palimpsest). A primary control on environments is the position of bedrock ledges and islands. Second are the glacial-glaciomarine sources of sediments. Third is the importance of sea-level lowstand shorelines and the Kennebec Paleodelta, a point source of sand and gravel on the west-central Maine coast. Finally, modern wave and tidal processes, biological activity, and human impact redistribute and rework these sediments. Three main environmental settings are recognized: 1) Rock ledges are swept clear of sediments, but accumulate talus aprons and halos of carbonate-rich coarse-grained gravel around their bases. 2) Nearshore ramp/paleodelta sandy environments are also above storm wave base, and are swept clear of mud (annually?). Their surfaces are reworked into sand waves, sand ribbons, and rippled scour depressions. 3) Basins are filled with thick Quaternary mud, and presently are slowly accumulating fine-grained organic-rich mud, which is bioturbated extensively. These basins are the locus of natural gas deposits, which occasionally vent to the surface, initiating gas pockmarks that are modified by organisms and currents. Identification of meter to ten-meter scale variability in sedimentary environments implies that great care is required for remote sediment sampling. Similar variability might be expected in benthic biological studies of the area.

INTRODUCTION

The inner shelf of the Gulf of Maine is characterized by heterogeneous bottom types, ranging from rocky outcrops to sandy slopes and soft muddy bottoms. The distribution of these environments is related to a combination of glacial and deglacial processes, changes in relative sea level, and nearshore sedimentary processes which have acted over the past 14,000 years. The purpose of this paper is to describe some aspects of the distribution of these sediments and the sedimentary processes that have formed them, as determined from a combined manned submersible and remote sensing/sampling study.

For the past six years our marine geology-sedimentology group at the University of Maine has undertaken detailed sedimentological investigations of the inner shelf using high-resolution seismic reflection profiling, side-scan sonar surveying, grab sampling, and limited coring. Since 1984, we have used NURP submersibles to compare direct observations with this remotely collected data. The study has evolved from an observational approach to, in 1987, an experimental one in which sediment traps and metric arrays were deployed for the analysis of bedform movement and suspended sediment fluxes. The seismic and sediment sampling have allowed detailed determination of late Quaternary stratigraphy, relative sea-level changes, paleogeography, and sediment distribution. The addition of direct observations and experiments from submersibles has allowed us to make preliminary inferences concerning sedimentary processes involved in sediment movement and long- and short-term rates of redistribution. The model developed suggests that the inner shelf of the Gulf of Maine is a complex, mixed process zone. The sediments are a palimpsest (see: e.g., Swift et al., 1972), showing evidence of former processes such as glaciation, which brought the sediments to the area, but also manifesting more recent reworking. This reworking was caused by fluvial and littoral processes during sea-level changes, by waves, tides, and mass-movement in the inner shelf environment, and by biological activities of bioturbation, formation of mats, and in situ production of carbonate.

Geologic Setting

The inner shelf of the northern Gulf of Maine (Figure 1) is underlain by Pre-Cambrian to Paleozoic metamorphic rocks and Paleozoic to Mesozoic igneous intrusive rocks (Osberg et al., 1985). The bedrock is overlain by Quaternary sediments, which have been described primarily by seismic stratigraphy (Belknap, 1987; Belknap et al., 1987a,b; Birch, 1984; Kelley et al., 1986, 1987a,b; Knebel, 1986; Knebel and Scanlon, 1985). The bedrock is directly overlain by thin till, with occasional moraines. These are covered by glaciomarine sediments, which are offshore equivalents of the Presumpscot Formation (Bloom, 1960, 1963). The glaciomarine sediments are muddy, with thin sand lenses and interfingering stratified subaqueous outwash. The glaciomarine

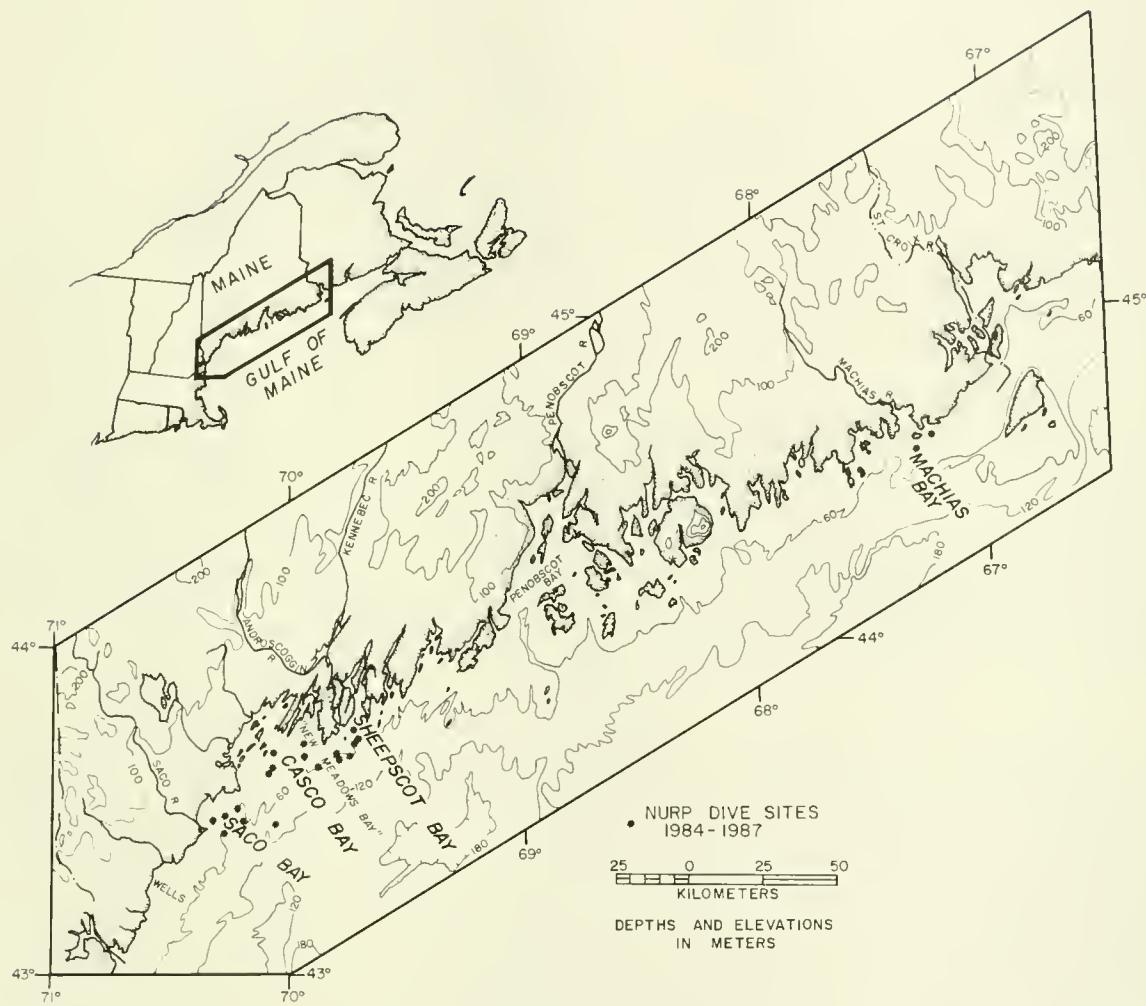


Figure 1. Location map: Maine coast, showing NURP submersible dive sites in Machias Bay, Sheepscot Bay, Casco Bay, and Saco Bay.

sequence is capped by an erosional unconformity down to at least 65 m below present sea level (Belknap, 1987; Belknap et al., 1987a,b), and overlain by Holocene littoral, deltaic, and marine basin deposits in various locations.

The events which produced this sedimentary sequence began with glaciation of the Gulf of Maine, prior to 20,000 years before present (yrs. B.P.), when the Late Wisconsinan Laurentide ice sheet extended to Georges Bank (Schlee and Pratt, 1970). Deglaciation was underway by 18,000 yrs B.P. (Hughes et al., 1985; Denton and Hughes, 1981). Schnitker (1975, 1986) suggested that the early stages of deglaciation occurred with an ice shelf in the Gulf of Maine. This ice shelf or a tidewater ice margin was grounded just offshore of the present coast by 14,000 yrs. B.P. (Smith, 1985; Stuiver and Borns, 1975), at which time it became a tidewater calving embayment (Belknap et al., in press). Deglaciation through tidewater calving continued until 13,000 to 12,500 yrs. B.P., while the sea onlapped present coastal Maine up to the marine limit 60-132 m above present sea level (Thompson and Borns, 1985). Sea level then fell rapidly (Figure 2; Belknap et al., 1986, 1987b; Schnitker, 1974) to 55-65 m below present as glacioisostatic rebound dominated. The rebound was greater to the northwest, tilting the highstand shorelines. A low stillstand occurred around 9500 ± 1000 yrs. B.P., as isostatic rebound and eustatic rise became equal, producing shorelines (Shipp et al., in press). Over the past 8000-9000 years the inner shelf has experienced a transgression, with relative sea level rising at a decreasing rate. Thus, the study area has undergone deglaciation, deepwater marine onlap, regression with its accompanying littoral and fluvial erosion, and finally the ongoing marine transgression with littoral and inner shelf processes of sediment redistribution.

Maine is in a cool temperate locale, with continental and oceanic regimes competing to produce a variable climate. Long-term wind and wave data for the central Gulf of Maine are summarized in Figure 3, from Summary of Synoptic Meteorological Observation (SSMO) statistics (USNWSC, 1975). Prevailing winds during summer are from the southwest, prevailing winter winds are northwest, and dominant storm winds are easterly or northeasterly (Fefer and Schettig, 1980). Waves with the longest period and greatest height are generated by winter storms, and thus come from the east and northeast, while the greatest exposure to fetch is from the southeast. Storm waves of 8-10 sec period and 3-4 m height are common during extratropical cyclones ("northeasters"), comprising 3.4% of the February waves in the central Gulf of Maine (USNWSC, 1975). Hurricanes, however, are rare (<5% annual probability: Fefer, and Schettig, 1980). Pearce and Panchang (1983, Figure 24) calculate the 50-year significant wave height to be 9.3-9.8 m off central coastal Maine, while the annual significant wave height is 3 m. Mean annual deepwater wave height is 1.13 m (Figure 3), while the August value is 0.68 m and the February value is 1.53 m. Tides are meso- to macrotidal, increasing in spring range from 3.1 m in Portsmouth

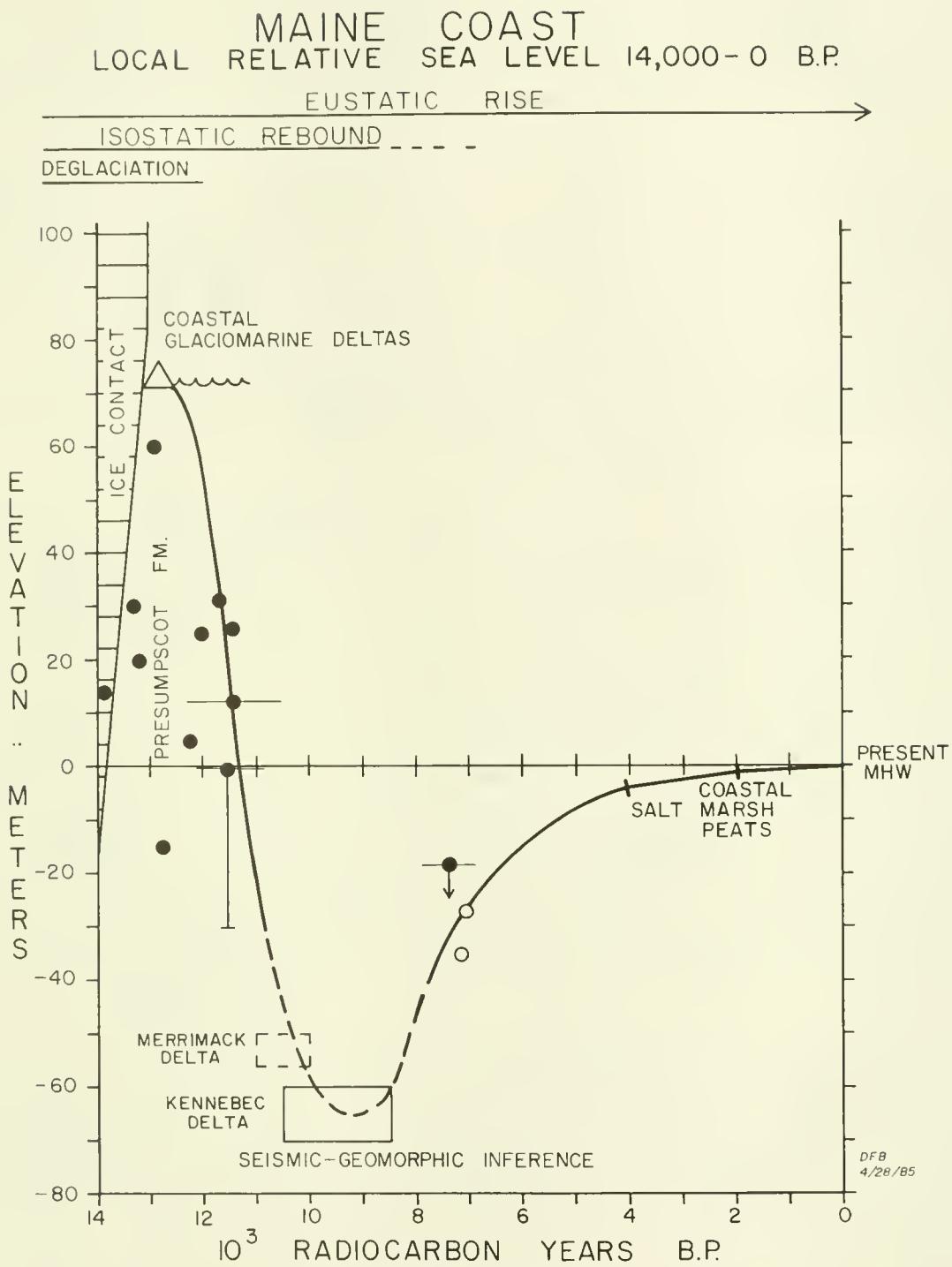
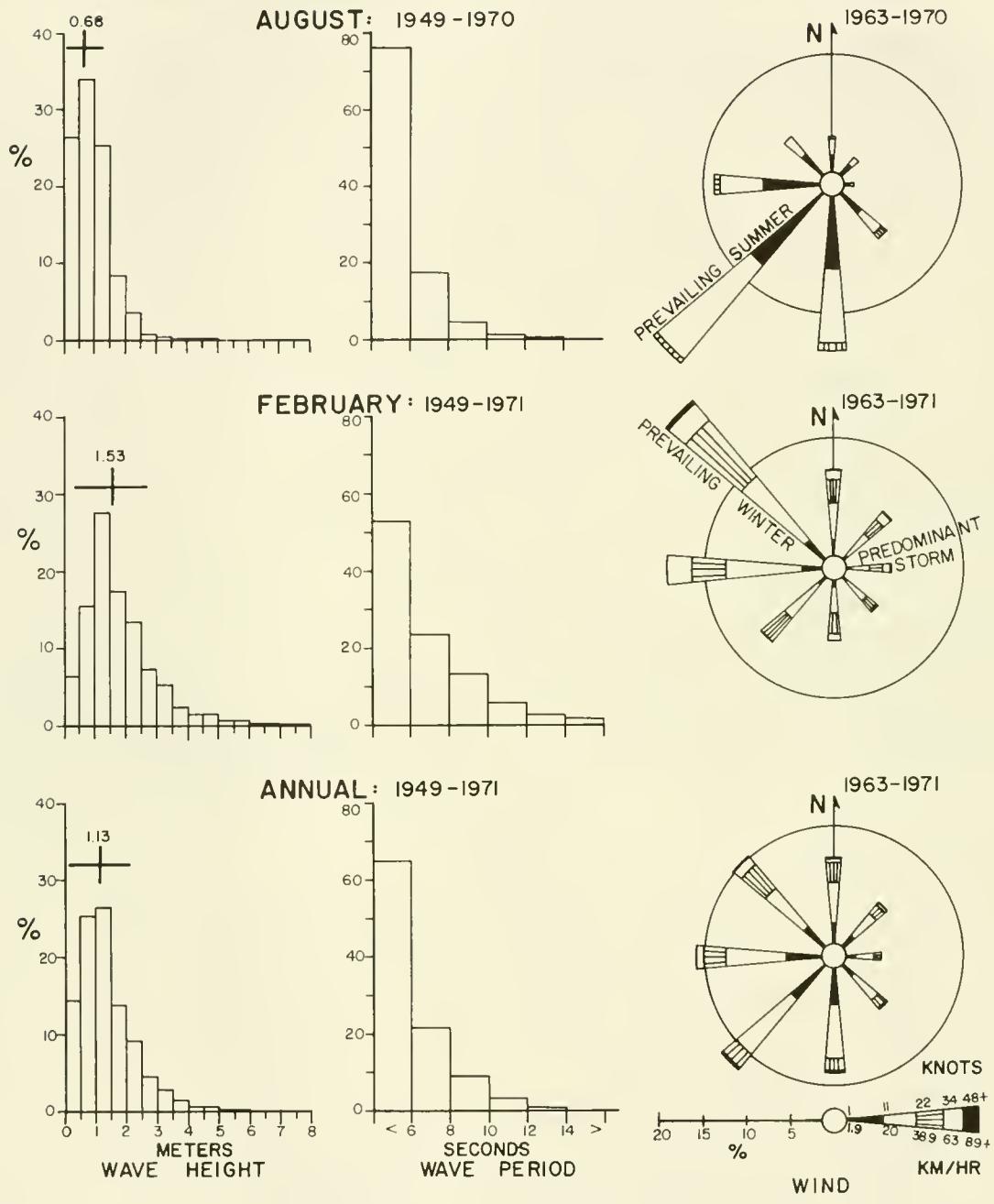


Figure 2. Late Quaternary sea-level curve for coastal Maine, from Belknap et al. (1986, 1987b)

SSMO DATA
CENTRAL GULF OF MAINE : 43.1°N 67.7°W



SSMO DATA USNWS, 1975 (V2, AREA 12: BOSTON)

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Figure 3. Rose diagrams of winds, histograms of wave heights and periods for central Gulf of Maine, compiled from Summary of Synoptic Meteorological Observations (SSMO) data, USNWS, 1975 (V2, AREA 12: BOSTON).

to 6.4 m in Eastport (NOS, 1987a). Tidal current velocities are variable, depending on local bathymetry, but are typically 0.5 knot (0.25 m/sec) in the open nearshore off the central Maine coast, increasing to more than 2 or 3 knots (1-1.5 m/sec) in embayments (NOS, 1987b). Runoff in rivers is concentrated in two peaks, a primary spring event and secondary fall event.

Maine's rivers are generally low in turbidity, except during the spring maximum. Extreme events, such as the greater than 100 year flood of April 1, 1987 (Hasbrouck, 1987) can bring considerable sediment to the nearshore. Peak flows from the combined Androscoggin and Kennebec Rivers at that time were 9,118 m³/sec, as compared to normal flow of 331 m³/sec, 27.5 times as great. Goldschmidt and Stumpf (1988) have shown, in satellite photos from April 2, 1987, an extensive sediment plume extending from the mouth of the Kennebec trending southwest over the west-central Maine coast, with peak turbidities as high as 30-100 mg/l.

Sediment supply to and from the coastal zone has been a subject of some discussion. Limited oceanographic data by Graham (1970) suggests an alongshore net southwesterly shelf drift, while Schnitker (1972) called for offshore sources of mud to the Montsweag Bay part of the Sheepscot estuary. McAlice and Jaeger (1983) used current meter and salinity measurements to show the variation from well mixed to partially stratified conditions in the Sheepscot River estuary. FitzGerald and Fink (1987) found similar conditions in the Kennebec River mouth, indicating well-stratified estuarine circulation only in spring. Farrell (1970), however, indicated that the Saco River is stratified at all stages of flow. Belknap et al. (1986), Kelley (1987) and Shipp et al. (1987) suggest that sediment is recycled within the estuaries during transgression, that offshore sources are not required, and that in fact some fraction must be lost offshore. Hay (1988) has completed a sediment budget for Casco Bay demonstrating a large net loss to the offshore during the Holocene transgression.

To our knowledge, no other submersible-based observations of sedimentology have been made in Maine prior to this study. Considerable work has been done in southern New England (e.g. Valentine et al., 1980; Ryan et al., 1978). Limited grab sampling associated with seismic profiles has been published (Folger et al., 1975; Ostericher, 1965), but the present Minerals Management Service project by the Maine Geological Survey (Kelley et al., 1987a,b) is the most comprehensive data set available. Cores have been collected in the estuaries (Belknap et al., 1986; Hay, 1988), but only limited core data is available offshore (Kelley et al., 1986; Schnitker, 1974).

METHODS

The approach to this study was to use existing seismic reflection, side-scan and sample data to compare with submersible

observations. High resolution seismic reflection profiling, discussed in detail by Belknap et al. (1986, 1987a), involved 3.5 kHz Raytheon tuned transducer and ORE-Geopulse boomer systems. The data has been interpreted in terms of intensity and geometry of reflections to form a consistent local stratigraphic model (Belknap et al., in press). Sediment process indicators, interpretable from the seismic data, include slumping, bedforms, topset/foreset contacts, natural gas deposits, and rhythmic bedding. The nature of the sediments could be estimated based on correlation with cores, grab samples, submersible observations and outcrops. The seismic reflection data were used to produce a seismic facies map (Figure 4), as well as interpreted cross sections.

A second major remote sensing tool is the side-scan sonar, an EG&G SMS 260 Sea Floor Mapping System. Backscattered sonar signals are digitally rectified into a true-ratio scale that is compensated for slant range and ship speed. The pixels are printed in a broad-band gray scale, producing an image analogous to an aerial photograph. These images are relatively easy to interpret and to form into mosaic maps. The side-scan images are used to identify sediment and bedrock features, process markers such as bedforms and slumping, and to locate submersible dive sites.

Investigation of sedimentation rates and seasonality of sedimentation is essential to the study of the nearshore environment. Two techniques were used, shipborne sampling, with a Smith-MacIntyre grab sampler (Kelley et al., 1987a,b), and submersible-manipulated sampling techniques. Smith-MacIntyre grab samples were collected during 1986 and 1987. Samples were described for grain size and fauna, and then stored for laboratory analysis. Over 1000 samples have been collected from southwestern and central Maine (Kelley et al., 1987a,b; Kelley and Belknap, 1988). Only a small percentage of these have yet received a complete grainsize and compositional analysis. No cores are yet available from the present series of studies. Submersible manipulated sampling included scoop samples with the manipulator arm, and a few experimental manipulations with box cores and tube cores. Neither of these techniques were used extensively. Preliminary sampling of suspended sediments was accomplished in 1987 using sediment traps of our own design (Figure 5). Two pairs of sediment traps were deployed on the Kennebec River paleodelta (Belknap et al., 1986) in Sheepscot Bay, and two pairs were emplaced in Saco Bay (Figure 1).

The sediment trap array bases are triangular, with a 2 m base, constructed from 5 cm PVC pipe, and filled with concrete (Figure 5). The hypotenuse leg was marked into decimeter segments to facilitate measurement of bedforms and photographic monitoring of their movement. Vertical legs were installed on the two short sides of the triangle to support sediment traps. The traps themselves are removable, for emplacement and removal by submersible. Each was constructed of 10 cm diameter by 30 cm

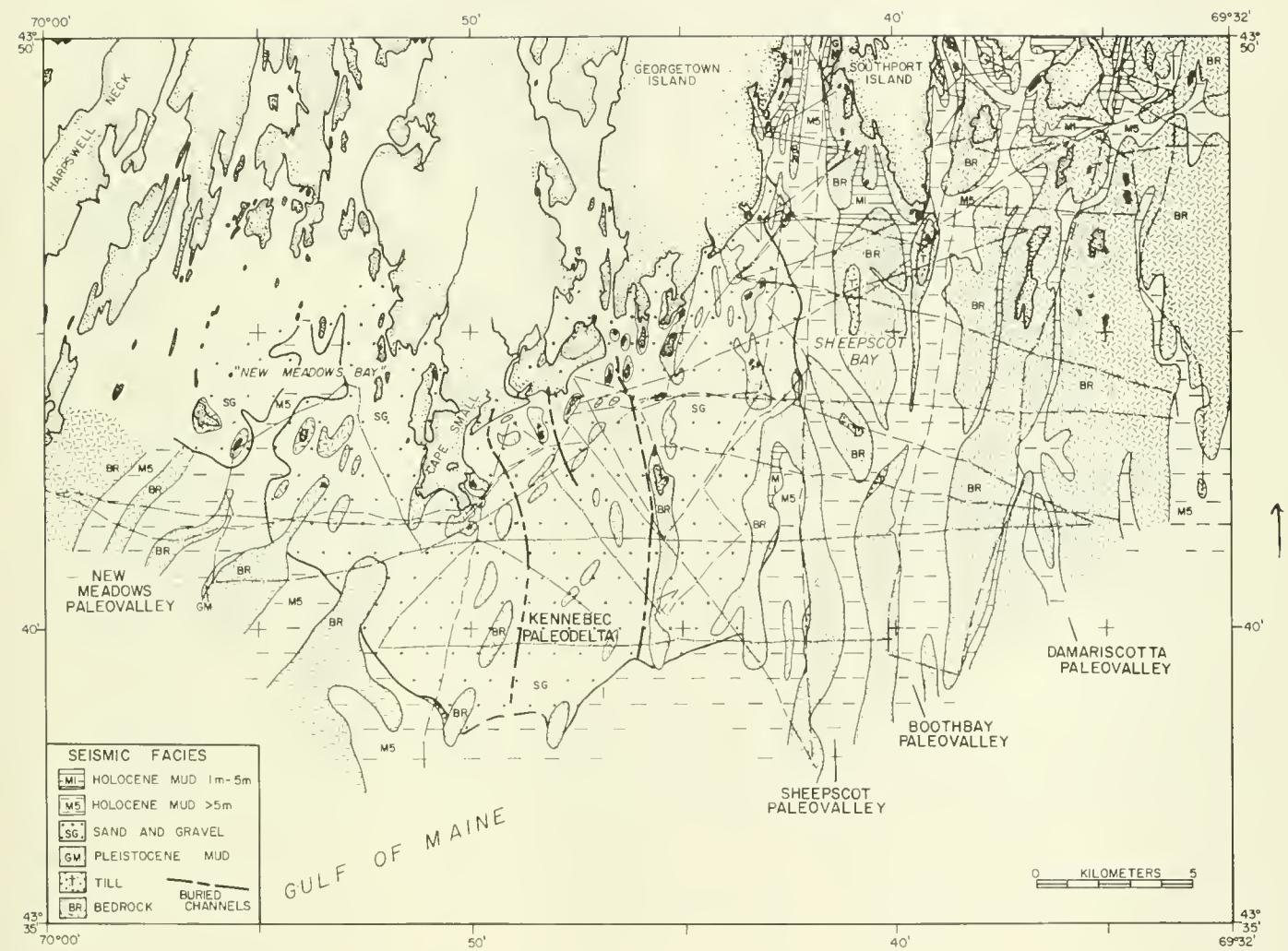


Figure 4. Summary of sedimentary environments for Sheepscot Bay, Small Point and eastern Casco Bay ("New Meadows Bay"), based on seismic reflection profiling, from Belknap et al. (in press). Seismic track lines shown with a dot-dash line pattern.

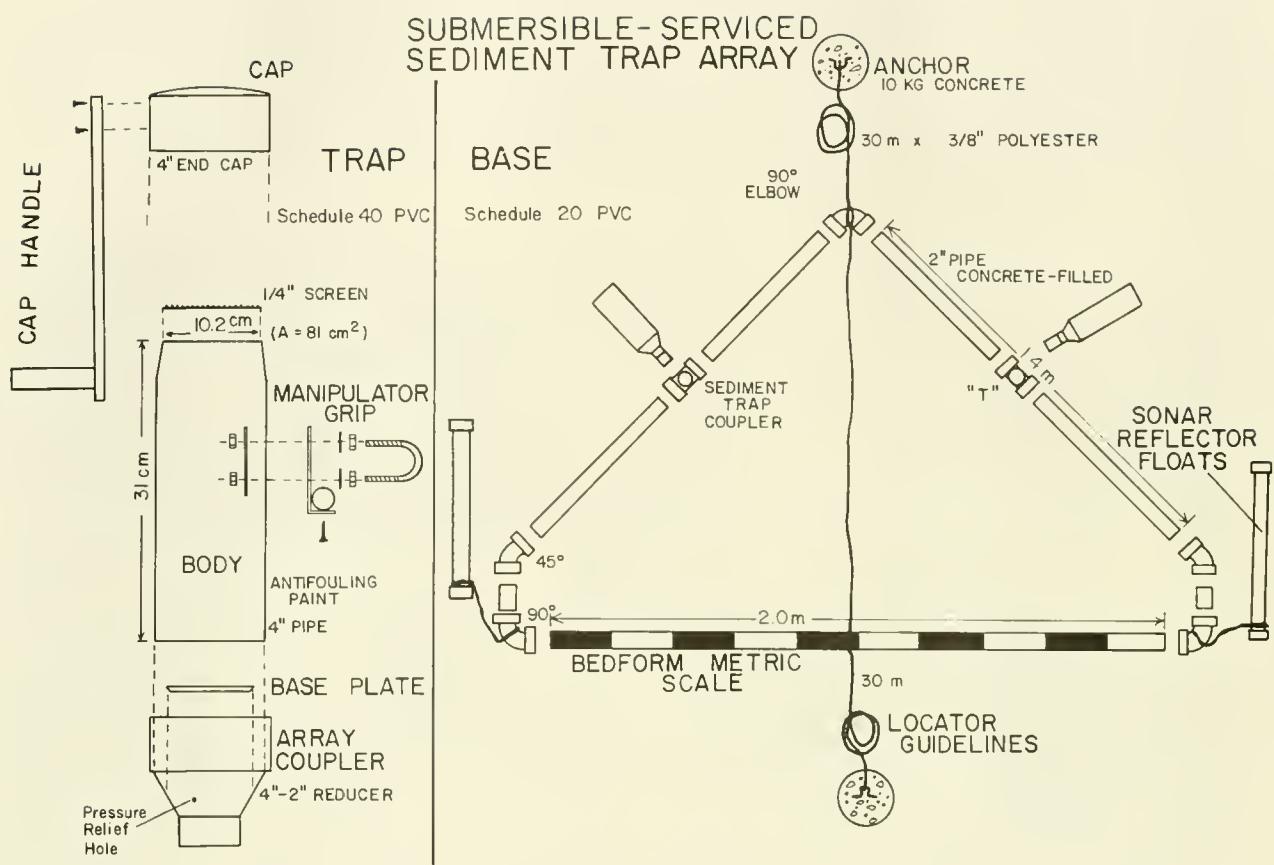


Figure 5. Schematic diagram of University of Maine submersible-serviced sediment trap array (right) and detachable traps (left). Major components are constructed of polyvinylchloride (PVC) plastic plumbing supplies.

length PVC pipe, sealed at the base, with a removable cap, and fitted with a handle for the submarine's manipulator arm (Figure 5).

The arrays were deployed from the surface after sites were chosen using side-scan sonar imagery. The arrays were attached to 60 m lengths of anchored line, stretched out laterally during deployment (practical in the <60 m depths selected). After deployment, the "Delta" submersible descended and searched first for the aligned anchor line, and then followed it to the array. Future surveys would be more practical if a pinger were attached to the array. Upon location of the array, the traps were installed, uncapped, and the site was photographed (Figure 6), paying particular emphasis to bedforms. The Kennebec paleodelta arrays were emplaced in June, 1987, and revisited one month later, at which time the traps were collected and replaced. The Saco Bay arrays were emplaced in July, 1987. All arrays will be revisited in the summer of 1988.

Sediment samples were analyzed by standard sieve techniques (sand fraction), and by Micromeritics Sedigraph 5000 ET (mud fraction). Sediment trap samples were pre-treated with bleach to remove organics. Size statistics were calculated with our laboratory program "LGRAIN" (Belknap, unpub.), which yields Folk-Ward and Method of Moment statistics.

Finally, direct observations of the sedimentary environments were made through submersible observations. Twenty-nine dives over the past four years have traversed more than thirty kilometers of sea floor (Table 1). Still photos, annotated videotapes, and logs of personal observations comprise the record of these dives, which are on file at the University of Maine. Most dives were directly along traverses that had previously been studied by seismic reflection profiling and/or side-scan sonar.

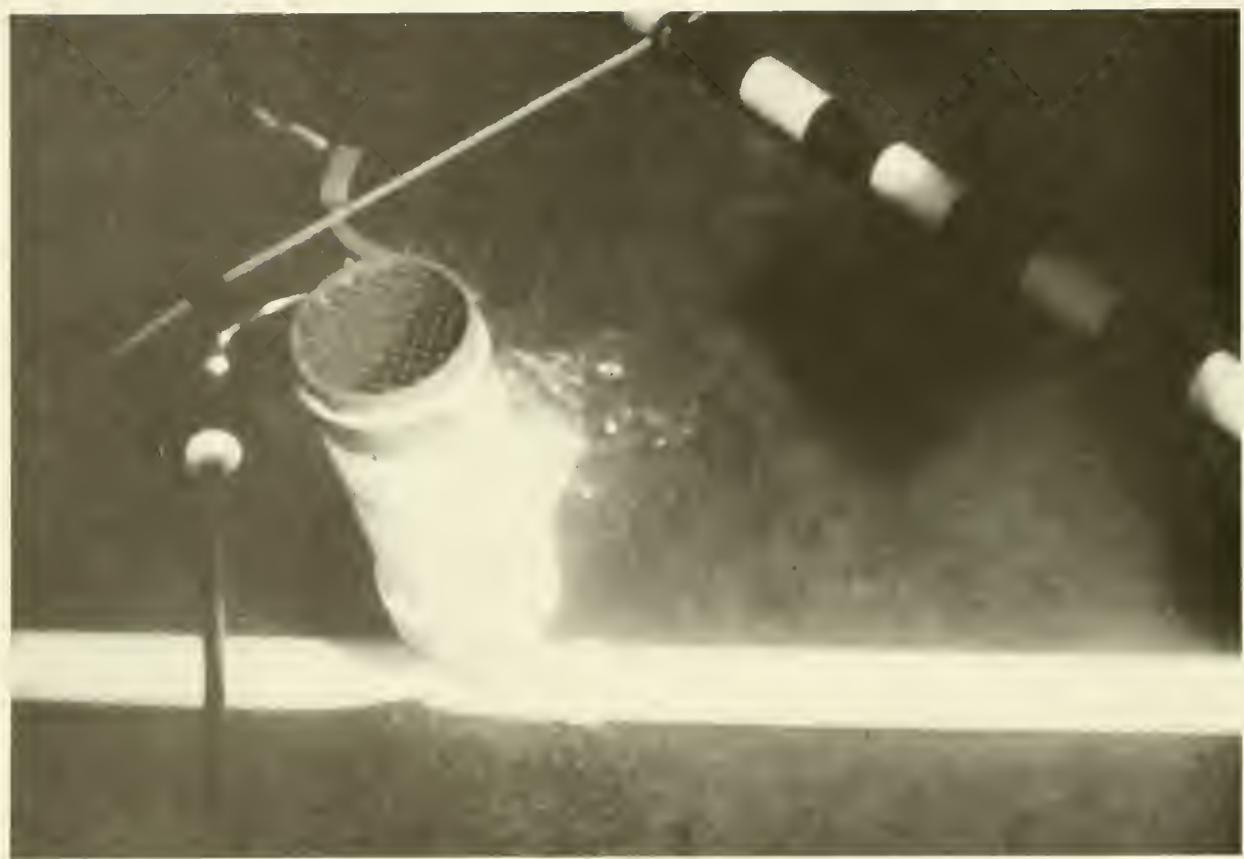


Figure 6. Photograph of sediment trap and array base in place at site SB-1, off Seguin Island in Sheepscot Bay. Note the manipulator arm of the Submersible Delta, and the crest of a megaripple in coarse sand near the base of the trap.

Table 1. Year, dive numbers, locations, and submersible systems utilized.

Year	Dive No.	Location	Submersible
1984	R7, R8 M-9	Sheepscot Bay Sheepscot Bay - Tom Rock	ROV Mermaid-II
1985	NURP-85-15	Machias Bay - Libby Island	Johnson Sea Link (JSL)
	NURP-85-16	Little Machias Bay	JSL
	NURP-85-17	Sheepscot Bay - Tom Rock	JSL
	NURP-85-18	Casco Bay - Halfway Rock	JSL
	NURP-85-19	Saco Bay - Richmond Island	JSL
1986	NURP-86-1	Sheepscot Bay - Seguin I.	Delta
	NURP-86-2	South of Small Point	Delta
	NURP-86-3	New Meadows Bay - Wood I.	Delta
	NURP-86-4	New Meadows B.- White Bull I.	Delta
	NURP-86-5	Casco Bay - NW Halfway Rock	Delta
	NURP-86-6	Casco Bay - SW Halfway Rock	Delta
	NURP-86-7	SE Casco Bay	Delta
	NURP-86-8	Outer Saco Bay	Delta
	NURP-86-9	Saco Bay NE of Wood Island	Delta
1987	(June)		
	NURP-87-1, 2	Sheepscot Bay - Seguin SB-1	Delta
	NURP-87-3	Sheepscot Bay - Seguin SB-1	Delta
	NURP-87-4	Sheepscot Bay - Mile Ledge	Delta
	NURP-87-5	Sheepscot Bay - Mile Ledge	Delta
	(July)		
	NURP-87-6, 7	Sheepscot Bay - Seguin SB-1	Delta
	NURP-87-8	Sheepscot Bay - Seguin SB-1	Delta
	NURP-87-9	Sheepscot Bay - SE of Seguin	Delta
	NURP-87-10	Sheepscot Bay - SE of Seguin	Delta
	NURP-87-11	Saco Bay - Dredge Spoil Site	Delta
	NURP-87-12	Saco Bay - SC-1	Delta
	NURP-87-13, 14	Saco Bay - SC-2	Delta
	NURP-87-15	Saco Bay - Biddeford Pool	Delta
	NURP-87-16	Sheepscot Bay - Mile Ledge	Delta

RESULTS

Seismic reflection profiling, side-scan sonar seafloor mapping, sediment grab samples, and submersible crossings form the basis for interpretation of modern sedimentary patterns and processes on the Maine inner shelf. An area of concentration so far has been the Kennebec paleodelta (Belknap, 1985) in western Sheepscot Bay and the surrounding environments (Figure 7) (Belknap et al., 1986; in press 1988). Much of the paleodelta surface is composed of gravelly muddy sand, rich in carbonate shell hash. Seasonal variations of the surface aspect of the Kennebec paleodelta are expected. These may include mud drapes produced after spring runoff and seasonally shifting bedforms. Figure 8 shows textural analyses of five of the grab samples. There is evidence of progressive winnowing of finer materials, producing a coarser lag near the Kennebec River mouth and finer sands on the distal lobe surfaces. On the whole, however, the primary mode of fine, well-sorted sand is similar to the finer range of beachface sands from adjacent Popham Beach (L.K. Fink, unpublished data). Detailed analysis of the remainder of the sediment samples is in progress.

As seen in sidescan records, the sediments on the sandy ramps occur in three major types of appearance: 1) smooth, low reflectivity; 2) rippled surfaces; and 3) large-scale variations in light and dark return, either as streaks or lenticular bodies (Figure 9). Submersible dives over these features confirm that sidescan return 1 is unrippled muddy sand. Return 2 is clean gravelly sand in large-scale oscillation megaripples. They have straight to sinuous crests and common tuning-fork junctions, short crestlines (continuity 2-10 m), amplitudes of 20-40 cm, and wavelengths of 0.5 to 2 m. Their crests are symmetrical and sharp or rounded (Figure 10). Return 3 is difficult to distinguish in the submersible, where direct visibility is usually 5 m or less (video and photos are even more limited). It is interpreted as being composed of sand waves and/or current furrows and streaks.

The megarippled sands (return 2) occur in distinct low-relief depressions and near bedrock outcrops (Figure 11). They occur only on the paleodelta and on other nearshore ramps in Maine, above storm wave base. We interpret these as rippled scour depressions, as described by Cacchione et al. (1984) from central California. Features of this type have been identified in shelf environments as diverse as the northern Bering Sea (Hunter et al., 1982), western Mexico (Reimnitz et al., 1976), Onslow Bay, North Carolina (McIntyre and Pilkey, 1969), the Mid-Atlantic Bight (Swift and Freeland, 1978), off Long Island (Shipp, 1984), and the Rhode Island shelf (Morang and McMaster, 1980). They are produced by combined oscillatory and unidirectional flow in storm waves and downwelling currents. Black and Healy (1988), however, find similar features in less than 8 m water depth controlled solely by convergence of refracted waves. We suggest bedrock steering and constriction of

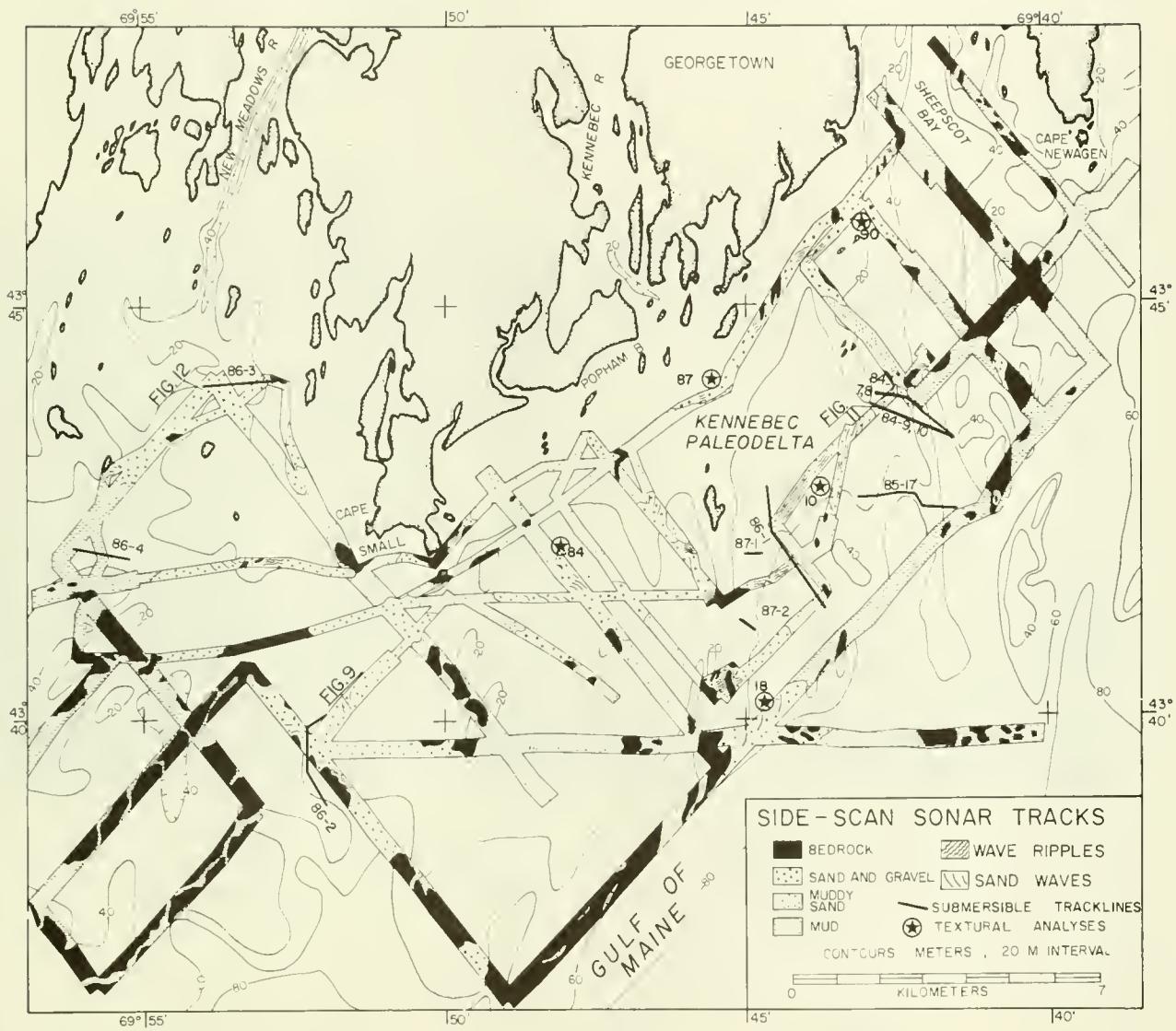


Figure 7. Side-scan sonar map of Sheepscot Bay, Small Point, and eastern Casco Bay area. Based on interpretation of EG&G SMS 260 and 960 data shown at true scale of coverage, grab samples, seismic reflection data (see Figure 4), and NURP submersible dives. Location of side-scan sonar samples (Figures 9, 11, and 12) indicated.

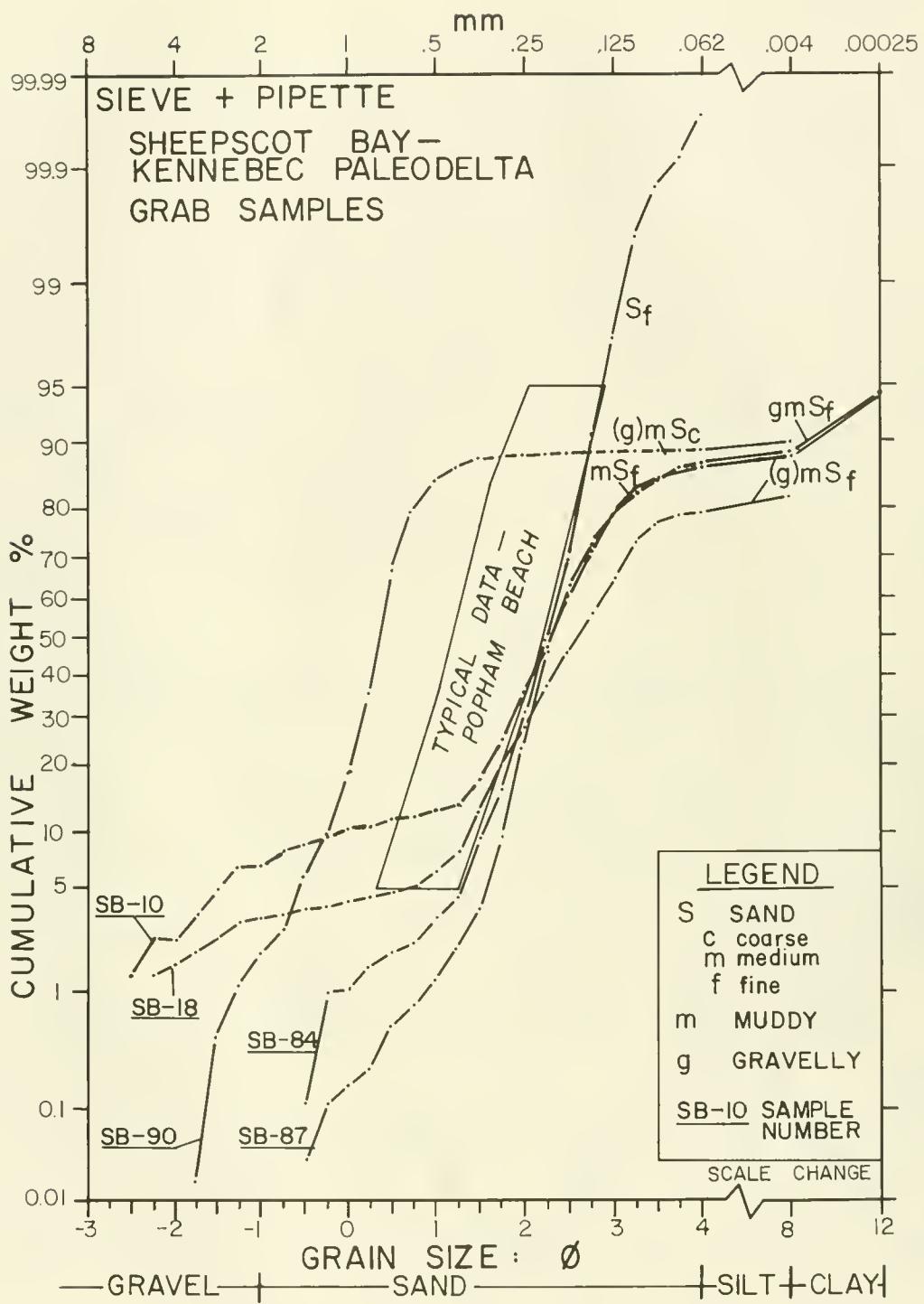


Figure 8. Textural analysis of surficial grab samples using sieve and pipette techniques, compared to typical Popham Beach sand data by L.K. Fink (unpub. data).

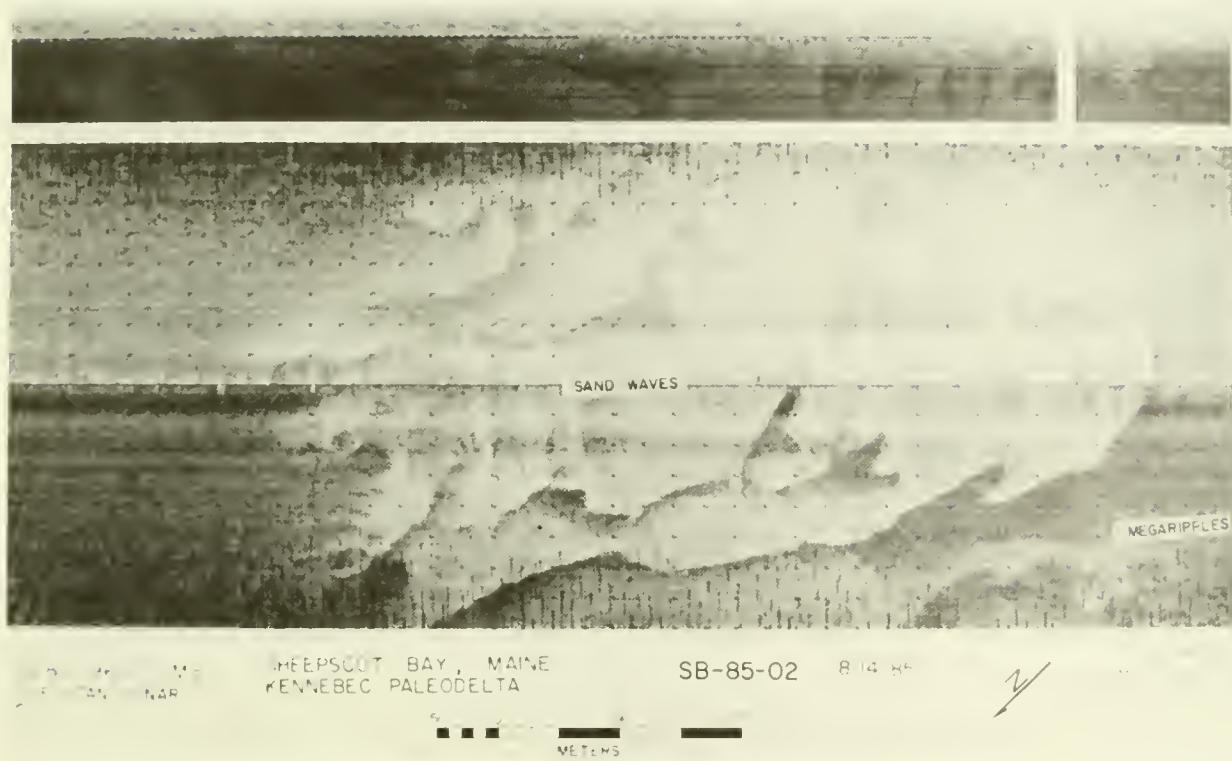


Figure 9. Side-scan sonar image from track SB-85-02, showing megaripples and sand waves on gently sloping paleodelta surface. Trackline is from right to left SW to NE in the center of the lower image (two digitally rectified channels). A vertical profile of the bottom is shown in the upper (third channel) image.



Figure 10. Submersible photograph of gravelly-sand megaripples, surface of Kennebec paleodelta, near Tom Rock (Dive 84-9, Roll 9, Photo 1-43). Crest-to-crest distance approximately 80 cm. Black quahog (Arctica islandica) approximately 8 cm diameter.

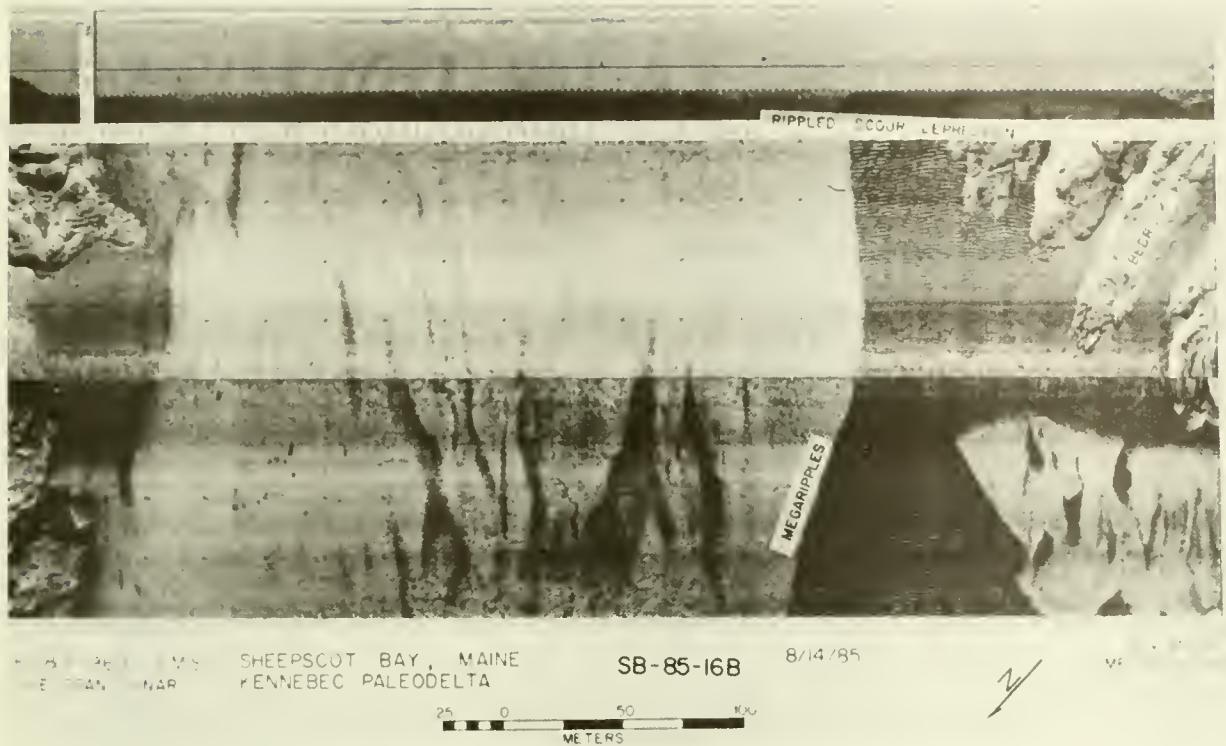


Figure 11. Side-scan sonar image of rippled scour depressions in coarse sand, associated with bedrock outcrops. Track line SB-85-16B. Same data format as Figure 9.

tidal currents as a contributing mechanism to the Maine features. Calculation of required waves for these megaripples is empirical, but based on Harms et al. (1982, Figure 2-10), winter storms of >8 sec period and >3 m wave height (Figure 3) are capable of producing the required 40 cm/sec near-bottom orbital velocities in 30 m water depth. Forbes and Boyd (1987) have reported on similar gravel ripples on the Scotian Shelf. They suggest that the ripples demonstrate a linear scaling to wave orbitals, and that published models may overestimate critical velocities for formation by a factor of two.

The deep paleovalley axes are sites of mud accumulation. Submersible observations reveal abundant molluscan, decapod and fish burrowing. In the upper 5 cm a "turf" of hydroids and amphipod tubes partially stabilizes the sediment surface. Lobsters and other decapods disturb the surface, both in individual burrows and in large shallow pits up to 5 m diameter and 0.5 m depth. We speculate, however, that natural gas seeps may initiate the larger depressions. These pockmarks show up prominently on some side-scan sonar lines, occurring only over gas-rich muddy basins. We have seen gas bubbles in the water column on fathometer traces taken while the side-scan sonar revealed the pits (Figure 12). Scanlon and Knebel (1985) have observed much deeper and broader pits in northern Penobscot Bay which might be a later stage of evolution of the postulated gas seeps. Similar large-scale features are seen on the Scotian Shelf (King and MacLean, 1970) and the North Sea (comparison of the two by: Hovland et al., 1984). Vilks et al. (1974) have discussed methane in sediments from similar settings off the Labrador shelf. Sedimentation in the deep basins is by pelagic settling and probably by periodic low-density turbidity currents. Bedrock ridges and the paleodelta are swept relatively clean of fine sediment by tides and waves. In addition, slumping occurs along channel margins, at least within the estuaries (Belknap et al., 1986; Kelley et al., 1986; 1987b).

Shipp et al. (in press) have demonstrated the presence of lowstand shorelines on the Maine coast based on four lines of evidence. These are: 1) location of prominent terraces in a zone from 50 to 65 m depth, 2) distinctly thinner Quaternary sediments above -65 m, interpreted as removal during lower sea levels by subaerial and littoral processes, 3) truncation of shelf valleys (lowstand paleovalleys) at -65 m, and 4) the depth of erosional unconformity to conformity transition in shelf basins (60-90 m, lowered sea level plus paleo-wave base). In submersible traverses across the postulated lowstand position in Machias Bay (NURP-JSL Dive 1985-15: Shipp et al., in press), we have observed coarser and better sorted materials in a narrow zone centered on a terrace feature at 55 m depth. Similar transitions occur off the Kennebec Paleodelta at the toe of foreset beds (Belknap et al., 1986). We searched for a similar transition in Saco Bay (NURP-JSL Dive 1985-19; Kelley et al., 1987a), but the terrace was draped with a sheet of mud.

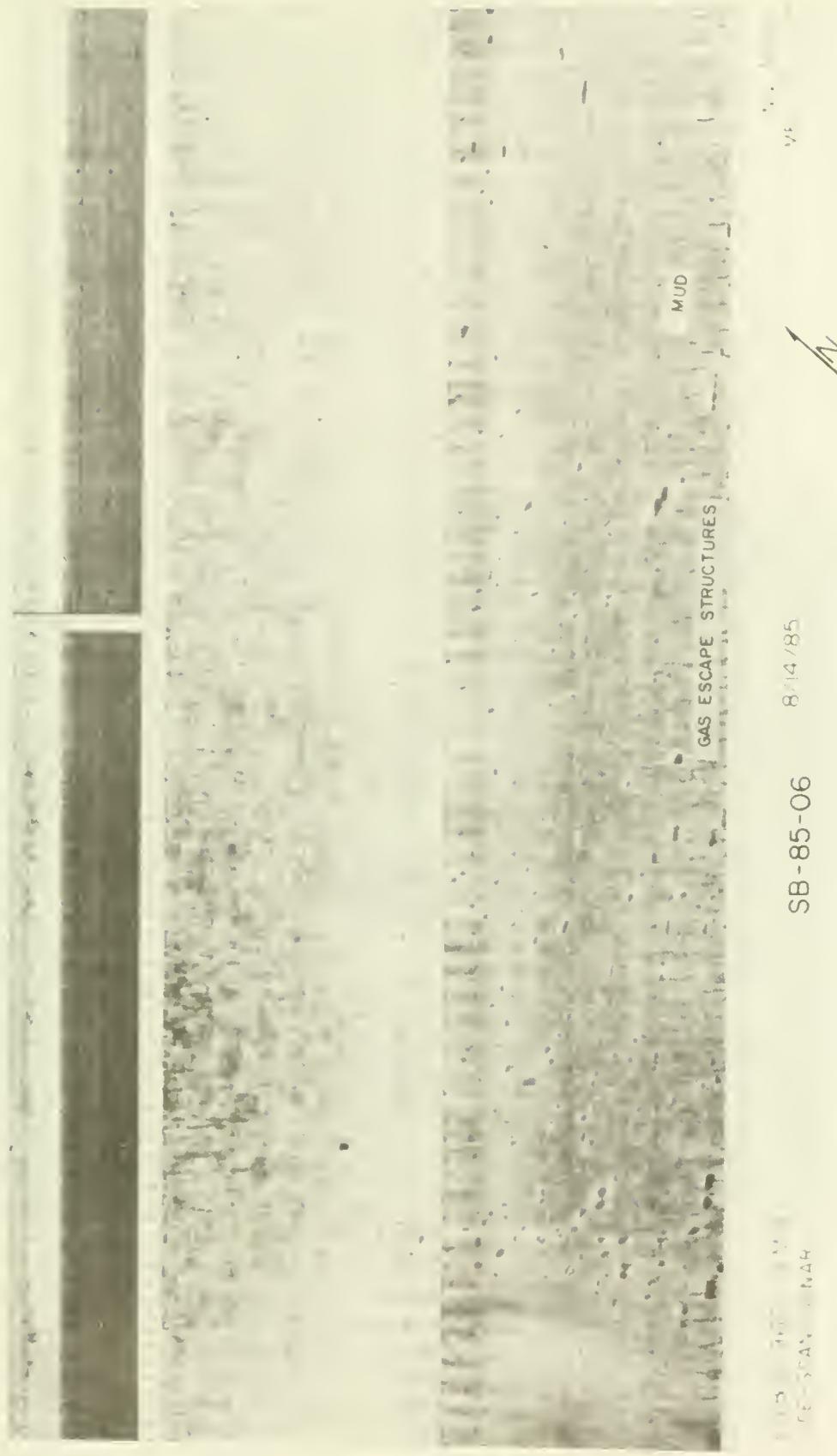


Figure 12. Side-scan sonar image from track line SB-85-86 in "New Meadows Bay." The dark ovals are pockmarks interpreted as gas escape structures modified by organisms and currents (?). Scale of the larger image is the same as Figure 11, 200 meters full cross-track width.

Throughout the course of four years of diving, a number of process observations have been made. The storm-generated gravel ripples have been discussed above. Concave-upward bivalve shells are found on the surface in many muddy basins. These are in a less stable position than if they were being swept by strong currents, and may represent either settling, death position after disarticulation by starfish, or bioturbation tipping. In any case, they argue for low current velocity and infrequent physical disturbance. Shells in talus aprons (Figure 13), on the other hand, are randomly oriented or convex upward, suggesting more vigorous current reorientation. There is a ubiquitous amphipod tube and hydroid mat or "turf" that stabilizes the mud surface in basins. Where this mat is disturbed by larger organisms, scour of fine-grained sediments is more likely. Bioturbation is ubiquitous, from deep, 10 cm diameter burrows in the muddy basins (Figure 14), to narrow worm and decapod burrows on the sandy surfaces. The relative degree of bioturbation is a measure of frequency of physical disturbance. Future studies will integrate this factor into sediment facies and process reconstructions similar to those by Howard and Reineck (1972). Finally, human disturbance is common in the muddy basins. Drag marks from trawl doors and rollers leave grooves a few centimeters deep and up to 20 cm wide. These can overturn rocks, rip up the "turf", and otherwise disturb the biota.

Pelagic settling was noted from the abundant "marine snow" in many of our dives. This may adhere and accumulate in the basins, but is not evident as a long-term build-up above wave base. Sediment samples recovered from the traps in 1987 are obviously only a preliminary indication of the suspended fraction, but they are consistent. Analysis of the inorganic fraction revealed mean grain sizes of 8.1 to 8.4 phi (Figure 15). Averaging the accumulation over the 23 day period suggests an accumulation rate of $0.5 + 0.2 \text{ g/cm}^2/\text{yr}$. This is consistent with submersible observations of a roughly 1 cm thick fluffy organic layer on the surface of much of the inner shelf. Under a microscope, much of the coarser part of this material is seen to be diatom tests and sponge spicules. This organic mud is not a permanent component of the sandy Kennebec paleodelta or sandy zones in Saco Bay, and is presumably reworked by winter storms.

We speculate that low-density turbidity currents may carry sediments into the deeper basins, especially when generated from submarine slumps. Kelley et al (1987a, Figure 22) and Belknap et al. (1986, Figure 4) have demonstrated the presence of active submarine slumps in the Maine nearshore. An examination for graded beds in cores, or detailed process studies with nephelometer and sediment traps will be required to demonstrate the turbidity current hypothesis, however.



Figure 13. Submersible bottom photograph of carbonate-rich talus gravel, Sheepscot Bay, near Tom Rock (Dive 84-9, Roll 8, Photo 5-24). Full scale of photo is approximately 80 cm width. Note scuplin in left foreground.



Figure 14. Submersible bottom photograph of bioturbated muddy bottom, Sheepscot Paleovalley (Dive 84-9, Roll 8, Photo 3-12).

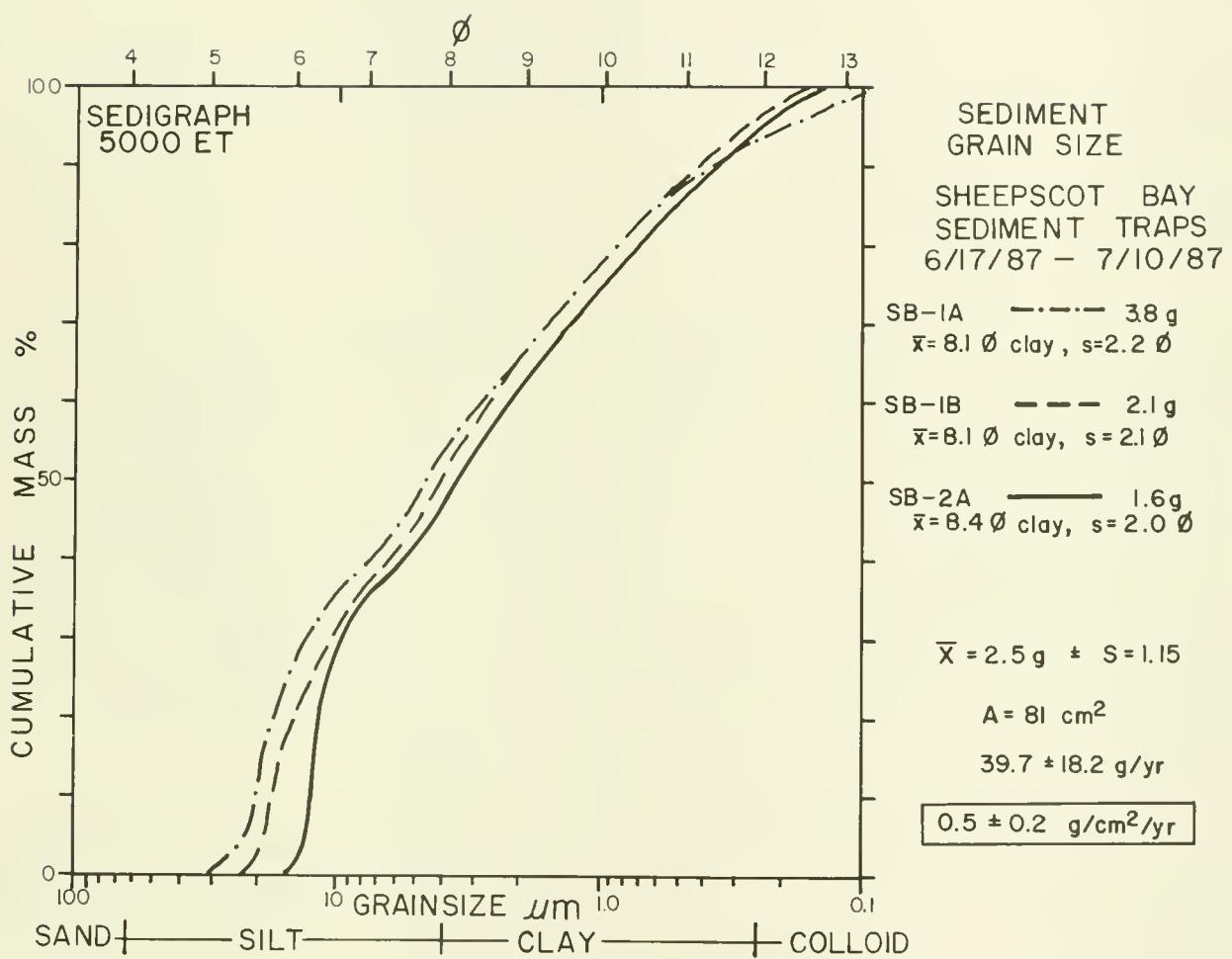


Figure 15. Textural analysis of one month's sediment trap collection, SB-1 and SB-2 arrays, Kennebec Paleodelta off Sequin Island. Analysis by Sedigraph 5000ET, an automated X-ray scanned settling cell system.

DISCUSSION AND CONCLUSIONS

The comparison of remote and direct observations has created a synthesis of sedimentary environments for the Maine inner shelf. Figure 16 summarizes some of the major characteristics which we have found using all of these techniques. The rock margin example figured here is based primarily on dives at Halfway Rock, in Casco Bay. Along rock margins sediments are swept clear by waves and tides. Anemones, sponges and other organisms cling to the rocks. Rocks are dislodged from the outcrop and carried through joint chutes or directly down the face to a talus pile. The talus is probably partially a relict on deeper outcrops, when the greater energy available from waves at lowered sea levels was available to dislodge rock fragments. We have not observed well-rounded beach pebbles, however. The talus pile of rock fragments adjoins a coarse apron composed of gravel and shells, primarily mussels (Modiolus modiolus), and accumulates at the base of steep faces around islands and shallow ledges. The carbonate fragments appear fresh, and probably represent a continuing balance of supply of shells from productive shallower regions versus corrosion in the cool seawater. Locally, till crops out on the sea floor. It is identifiable by large, well-rounded boulders at the surface.

The paleodelta example (Figure 16) is based on the Kennebec paleodelta in western Sheepscot Bay, observed at eight dive sites of fourteen kilometers cumulative extent. Sand and gravel are reworked periodically by storm waves and tides, sweeping away muddy pelagic drape. The coarse sediment is a relict of lowstand paleodelta deposits reworked from upstream glaciofluvial sources. The surface is formed into sand waves, ripples, sand streaks, and the large-scale rippled scour depressions. Thus, this surface is a palimpsest, with a imprint of modern processes over the relict deltaic and transgressive littoral paleoenvironments. During transgression, some of the sand has been reworked into the modern Reid Beach and Popham Beach barrier systems. There is little evidence for extensive transport of sand off the edge of the paleodelta into the deeper basins: the transition zone from sand to mud is a few tens of meters in most cases.

The basin example (Figure 16) is a composite based on dives in Casco Bay, Sheepscot Bay, and New Meadows Bay. The basin floor is soft mud with abundant bioturbation. There are frequent drag marks from trawls. The dominant natural processes on the basin floor are evidently bioturbation and quiet pelagic settling. Any turbidity currents or slumping must be infrequent or localized, since the abundant burrows and shells at the surface suggest a slow accumulation rate. Natural gas has been noted at depth in most of the nearshore basins, with pits possibly produced by seepage in Penobscot Bay and New Meadows Bay. The pits observed by submersible in New Meadows Bay, referred to as pockmarks, are shallow and actively reworked by lobsters, crabs, and most likely by fish. They are circular to elliptical, with scalloped edges. The sediment within the pits

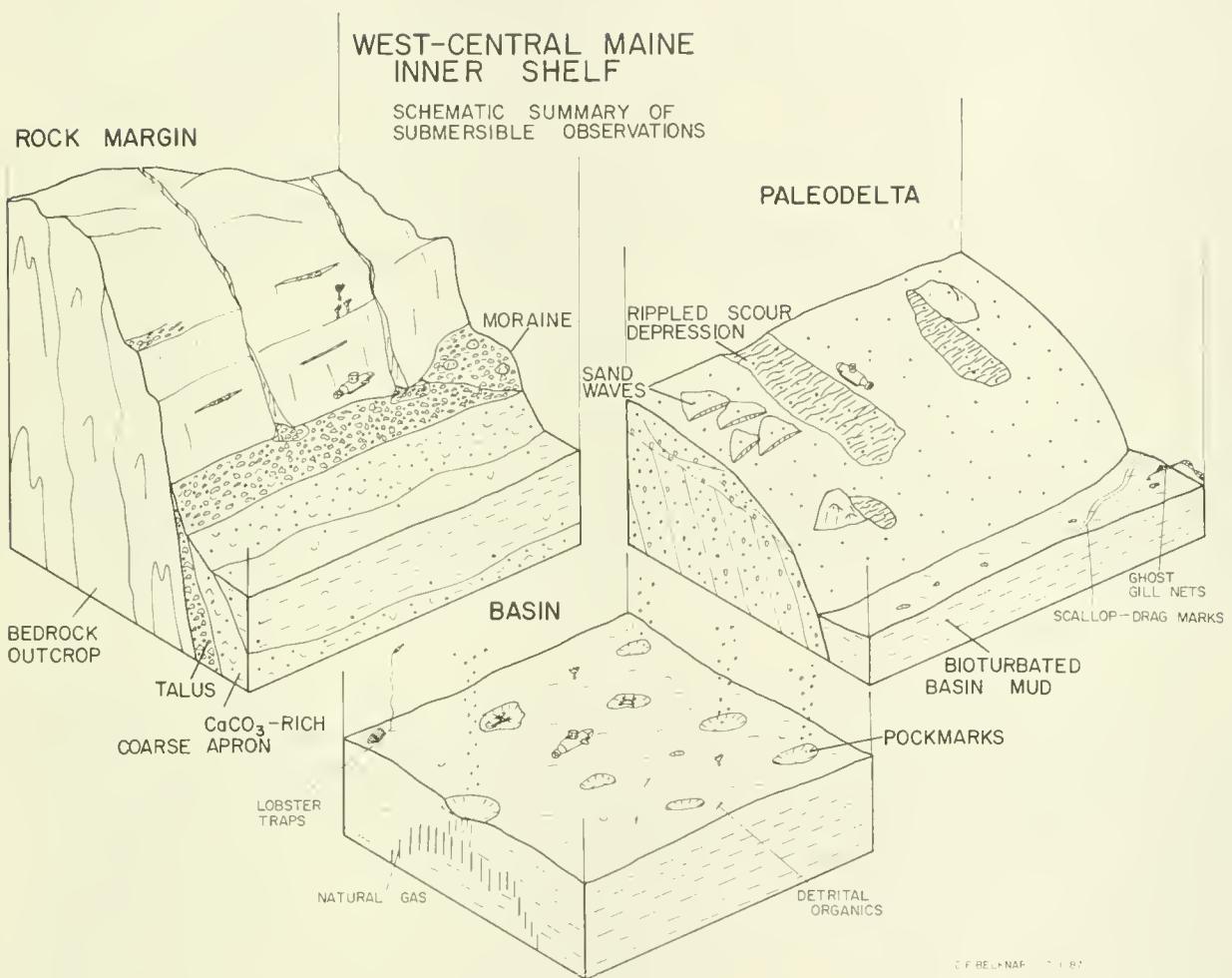


Figure 16. Schematic diagram of sedimentary environments based on remote sensing, sampling and submersible reconnaissance.

is loose, not stabilized by invertebrate "turfs", and may be more easily moved by currents. The lack of elongation suggests that current scour is not a dominant cause. The pockmarks are most likely complex features with multiple causes.

In summary, the inner shelf of Maine, in the areas we have observed by remote techniques and by direct submersible reconnaissance, is a patchwork mosaic of sedimentary environments. The greatest variability is above 60-90 m depth, that is above the depth of the early Holocene lowstand and paleo-wave base. Variability on the scale of meters and tens of meters is evident. Planning for future sediment grab sampling and biological sampling should consider this; one random sample per square kilometer does not give a fair assessment of the variability. In much of the area the sediments are a palimpsest of Quaternary sedimentary regimes overlain by modern processes. Glacial and deglacial, subaerial, deltaic, and shoreline processes may have acted on a specific locale before the present marine conditions took hold. We also have gained a better appreciation for the interaction between biological and geological processes here. Carbonate productivity around shorelines and shallow shoals has resulted in a carbonate halo. Bioturbation and microbial production of gas are important factors in basins. In the reverse application, the better definition of this mesoscale variability in geologic environments should be of use to biological oceanographers in evaluating the Maine inner shelf ecosystems. Finally, the integration of remote sensing, sampling, and direct observation and experimentation from submersibles has allowed a more complete determination of the distribution of and processes acting in these sedimentary environments.

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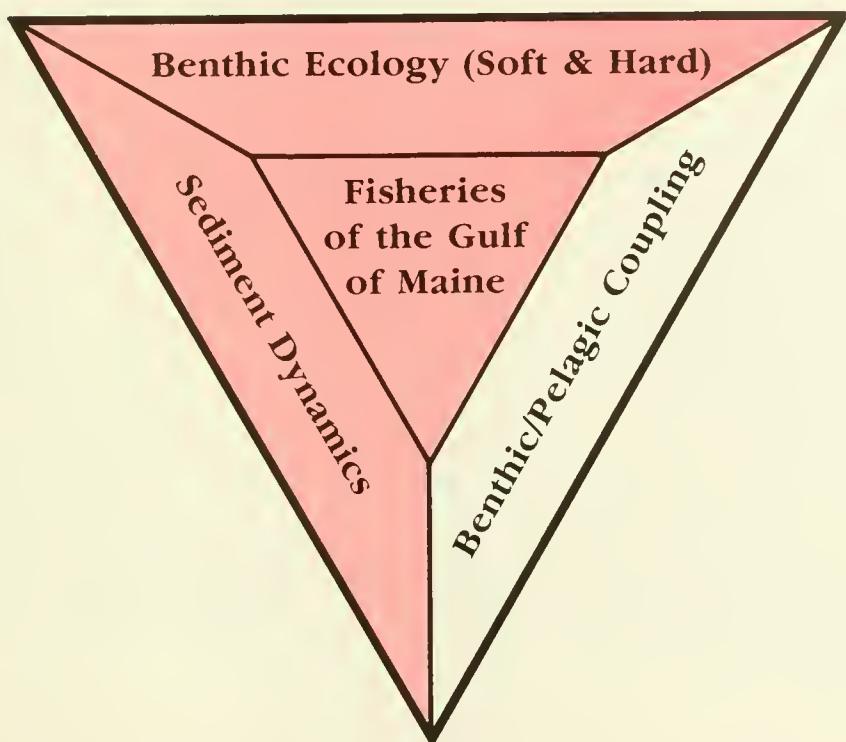
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Benthic-Pelagic Coupling



SESSION SUMMARY:BENTHIC-PELAGIC COUPLING

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Particulate organic materials (POM) are major food resources that can sustain marine food chains on the sea floor and in the water column. Two research groups, one from the Harbor Branch oceanographic Institution (HBOI) and one consisting of scientists from the Louisiana Universities Marine Consortium (LUMCON), the Bigelow Laboratory for Ocean Sciences (BLOS), and the University of Maine (UM), collaborated to make comprehensive measurements of the distribution, amount and flux of POM in order to permit predictions about the biological, chemical, and physical processes that affect POM accumulation, transport, and utilization. Specifically, the occurrence, density and composition of large (fecal pellets from zooplankton, HBOI) and small (LUMCON/BLOS/UM) particulate matter within the water column and near the sea floor were related to environmental discontinuities, mixed layer productivity and decomposition-dissolution processes. Submersibles (JOHNSON-SEA-LINK and DELTA) and conventional water bottles were used to selectively sample particles at water mass boundaries as well as the sediment/water interface. In addition, collections gathered with moored and free-drifting sediment traps provided estimates of daily POM flux rates. The information gathered should enhance the interdisciplinary mode of the Benthic Productivity Program in the Gulf of Maine. For example, knowledge of POM flux rates will contribute to understanding the patterns of distribution, abundance and survival among suspension feeders and deposit feeders.

Data from the HBOI group indicated that vertically sinking fecal pellets from a single euphausiid species Meganyctithanes norvegica can transport substantial amounts of organic matter to the bottom. Furthermore, vertically migrating populations of this krill, which feed on resuspended particulate material in the epibenthic nepheloid layer, may reintroduce such material into the mixed layer. Information from the LUMCON/BLOS/UM group revealed that particulate matter from the mixed layer and the nepheloid region were protein-rich. Biologically available protein in these two regions was 84 and 21% of the total protein, respectively.

Two of the most sophisticated devices developed to date to sample the fluff layer are described in Mayer et al. Future investigations of particulate materials will require the utilization of additional sampling devices that can be

deployed from surface ships and manned submersibles. Sequential sampling sediment traps that can collect data year round and multi-chambered fluff layer traps that can work at the sedimentwater interface are but two examples of technically advanced tools needed to advance hypotheses about the fate of POM. Staging missions in spring and early summer periods when primary production is likely to peak in the mixed layer will permit assessments of POM flux.

THE ROLE OF NEPHELOID LAYERS IN BENTHIC-PELAGIC COUPLING

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ABSTRACT

Particulate organic matter (POM) formed at the surface of the Gulf of Maine is concentrated as it sinks to the bottom in subsurface particle maxima and the bottom nepheloid layer (BNL). The hypothesis that these particle maxima are layers of intensified biological activity where substantial changes occur in the quantity and quality of the sinking POM is being tested by comparing the numbers of organisms, the chemical and biochemical composition and the physical and optical properties of the particles in the particle maximum layers with the intervening particle minimum layers. During a test dive in 1985 in the Sheepscot River estuary, chlorophyll, protein, bacterial numbers and SPM were measured on water samples taken at cm to m depth intervals above the bottom nepheloid layer (BNL) using the Johnson Sea-Link. In 1986, the particle maxima, BNL, and clearer water in between were sampled in Jordan Basin (250 m) and off Mt. Desert Island (100 m), using a bottom-tripping sampler with three, 30 l Niskin bottles or a rosette with CTD, beam transmissometer, and 24, 5 l Niskin bottles (from the R.V. Oceanus). Measurements included acetone-extracted chlorophyll, total and biologically available protein, CHN, ATP, respiratory electron transport activity, particle volume and size analysis, and counts of bacteria, autotrophic and heterotrophic nanoplankton, micro- and meso-zooplankton.

Some biological enhancement of almost all the particle maxima was observed. Since protein concentrations were the most consistently elevated, these particle maxima may be nutritionally enhanced. There was considerable variation in the biological and chemical properties of particles in the BNL between the two stations, between dates at the same station, and between replicates taken within several hours at the same station. Some of the variation could be explained by differences in hydrography or environmental conditions, and some is probably related to the dynamic nature of the processes in the BNL.

INTRODUCTION

Particle maxima, especially bottom nepheloid layers (BNL), are ubiquitous features in the world's oceans (McCave, 1986). They are hypothesized to be biologically enhanced over the surrounding clear water layers and to be major sites where organic matter degrades (Garfield et al., 1983; Karl et al., 1984; Fowler and Knauer, 1986). In the Gulf of Maine there are two or three particle maxima, depending in part on the presence of certain water masses (Spinrad, 1986). At deeper stations these include surface and intermediate particle maxima and a BNL, while at shallow stations only the surface maxima and BNL are observed. Organic material produced at the surface must pass through and be altered by these particle maxima before becoming a food resource for benthic organisms and demersal fishes. Accordingly, some organisms may feed selectively in particle maximum layers, due to the nutritional enhancement. In particular, the degree of biological and nutritional enhancement in the BNL may be a major factor affecting benthic productivity.

The nutritional quality and biological enhancement of particle maxima, especially the BNL, were determined at three sites in the Gulf of Maine in 1985 and 1986. In 1986, the major field year, Jordan Basin (A, Fig.1) was sampled on two dates and a station off Mt. Desert Island (B, Fig. 1) was sampled in the interim. The Jordan Basin station (approximately 250 m deep) is at the center of a cyclonic gyre which minimized horizontal advection. It is well stratified in the summer with low primary productivity in the surface and typically three particle maxima. The Mt. Desert Island station, in contrast, is much shallower (approximately 100 m), is well mixed with strong tidal currents near the bottom, has generally higher surface productivity and has only two particle maxima. In 1985 a station was taken in Sheepscot River estuary (C, Fig. 1, approximately 80 m depth) to sample very near the bottom. During 1985 sampling was accomplished with the Johnson Sea-Link submersible, but in 1986 sampling was conducted from a surface ship, the R.V. Oceanus, with sampling gear.

It was hypothesized that the surface layer, where primary production occurs, would be the most biologically enhanced. At the more nearshore Mt. Desert Island station it would be more enhanced than at the Jordan Basin station. The relative enhancement of the intermediate particle maximum cannot be hypothesized because it has been studied so little. Our efforts concentrated on the BNL. The strong gradients in particle concentration near the bottom suggest that there should be similar gradients in nutritional and biological enhancement and chemical composition. The BNL should be biologically enhanced over the clearer waters above. Due to constant resuspension of bottom sediments by tidal currents at the Mt. Desert Island station, it was hypothesized that the BNL there would be less biologically enhanced than at the Jordan Basin station, despite the higher surface productivity and shallower depth at the

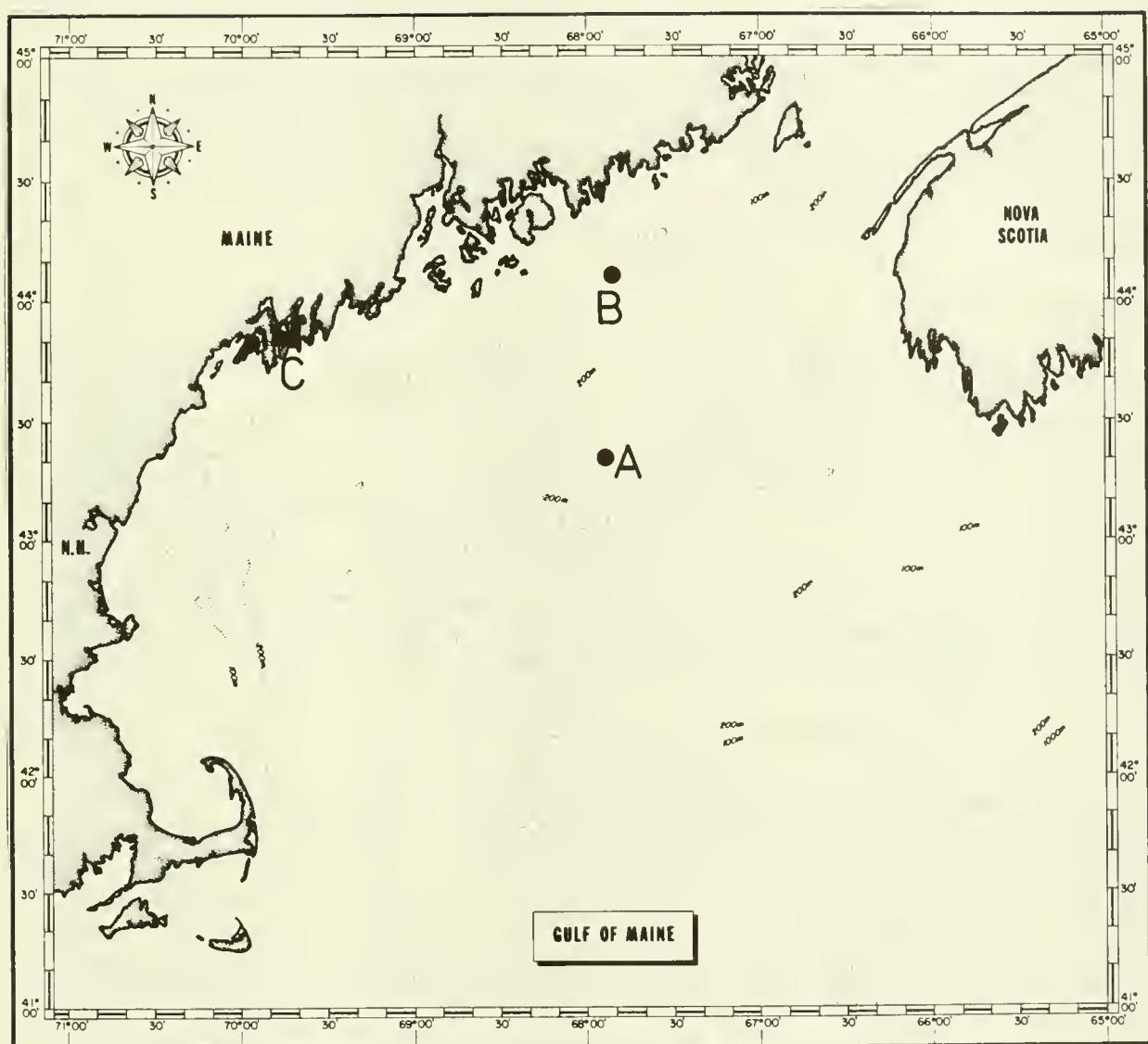


Figure 1. Station locations in the Gulf of Maine: Jordan Basin (A), Mt. Desert Island station (B), and Sheepscot River Estuary (C).

former.

Biological enhancement of particulate matter can be recognized by a variety of characteristics. The concentrations of biologically-derived compounds, such as protein or ATP, may be elevated. Ratios of chemical constituents, C/N, ATP/C, chlorophyll a/total pigment, will indicate the degree of degradation of the organic material present. Numbers of bacteria, autotrophic and heterotrophic nanoplankton, microzooplankton ($>35 \mu m$) and mesozooplankton will be increased. Finally, biological rates, as indicated by respiratory electron transport rates (Packard, 1986), will be elevated. Although these measurements can document biological enhancement, they cannot distinguish the mechanisms, which will be a combination of in situ growth, vertical (sinking from surface or resuspension from bottom) and horizontal transport with physical trapping, and migration of organisms.

METHODS

Sampling Methods

In 1985 water samples were obtained using the valve in the aft compartment of the Johnson Sea-Link submersible. It was connected via Tygon tubing to the robotic arm where a Sea Tech, Inc. transmissometer was also mounted. With the submersible sitting on the bottom and facing into the current, the robotic arm was positioned at various depths above the bottom, a reading was obtained with the transmissometer and water samples were collected in bottles in the aft compartment. To obtain samples at greater heights above the bottom, the submersible was slowly raised and then held stationary at the desired depth. Samples were filtered or preserved as soon as the submersible was back on board the ship.

In 1986 the submersible became unavailable at the last minute and the R. V. Oceanus was substituted. Two methods of sampling from the surface were utilized. A CTD with a transmissometer and a rosette with 24 5 1 Niskin bottles was used for measurements from the surface to 5 m above the bottom. (Identified by CTD in all figures). Although it could be used to obtain profiles in a very short time, the sample volumes were not adequate for more than a few analyses (chlorophyll, protein, heterotrophic and autotrophic nanoplankton) and it could not be used near enough to the bottom. To obtain large sample volumes between 2 and 20 m above the bottom, a bottom tripping rosette with 3 30 1 Niskin bottles was constructed (Identified by R in all figures). However, the rosette could sample only one depth at a time. Approximately 1-h elapsed between each cast at a particular station in order to process the water. Samples were filtered or preserved immediately.

Analyses

Water samples for analyses of the chemical and biochemical composition and enzyme activity in particulate matter were filtered onto precombusted (350°C, 12-h) GF/F filters (either 2.5 or 4.7 cm diameter depending on analysis) with vacuum <200 mm. Filters for ATP and acetone-extracted chlorophyll were extracted immediately. Samples for particulate C and N and biologically available protein were frozen over dessicant at -15°C and for total protein and ETS frozen in liquid N₂.

Acetone-extracted chlorophyll was measured fluorometrically according to Yentsch and Menzel (1963).

Particulate carbon and nitrogen were measured on a Carlo-Erba 1106 CHN analyzer.

Total protein was extracted with 10% trichloroacetic acid and analyzed by a modified Lowry method (Dortch et al., 1984). Biologically available protein is that part of particulate protein which can be degraded by protease (Mayer et al., 1986).

ATP was extracted by boiling filters in 0.125 M phosphate buffer with 4 mM EDTA and 20 mM MgCl₂ at pH 7.75 for 5 min. The samples were diluted back to their original volume, centrifuged, decanted into small vials and frozen at -15°C. They were analyzed using the firefly bioluminescence reaction (Karl, 1980).

Enzymatic respiratory electron transport activity was determined according to Packard (1986).

Organism Counts

Samples for bacterial counts were preserved with 4% buffered formalin and stored in the refrigerator until they could be counted. Cell numbers were determined on 10 ml samples from each depth using a DAPI stain and epifluorescence (Porter and Feig, 1980).

Autotrophic and heterotrophic nanoplankton were counted on the ship with an epifluorescence microscope and distinguished by chlorophyll autofluorescence and primulin fluorescence according to Caron (1983).

Microzooplankton and mesozooplankton were screened (35 μ m) from 70 l of water from the 3 30 l Niskins and preserved in 4% buffered formalin.

Particle Volume and Size Distribution

The particle volume and size distribution between 1.5 and 25 μ m were measured with a Coulter Electronics ZM particle analyzer.

RESULTS

Water Column Profiles

As expected there were three particle maxima in Jordan Basin and two at the Mt. Desert Island station (Fig. 2). The BNL at both locations was quite pronounced, although it was thicker at the Jordan Basin station. The position of the intermediate particle maximum in Jordan Basin shifted between the two sampling dates. Since it is usually found at the interface between Maine Intermediate and Bottom Water (identified by a change in salinity; Townsend and Cammen, 1985), it suggests major water movements could have occurred between the two sampling dates.

Samples for total protein concentration were collected during a number of casts in Jordan Basin, but since there were no obvious differences between the dates or the two sampling methods, the data have been combined in one profile (Fig. 3). Protein concentrations were elevated in all three particle maxima. The samples from the mid-water maximum were collected deliberately at the depth of minimum light transmission. In contrast at the Mt. Desert Island station, total protein concentrations may only be elevated in the surface layer.

The chlorophyll profiles (Fig. 3) at Jordan Basin were quite different from the protein profiles. There was a clear difference between the two sampling dates with generally higher chlorophyll concentrations on the second date. A major storm had occurred on September 16, just prior to the first sampling date, which may have eroded the nutracline, resulting in a fall bloom by the second sampling date. However, there is no way from the available data to distinguish between that and differences due to horizontal patchiness and water movements alluded to above. There was no evidence of elevated chlorophyll concentrations in the intermediate particle maximum, although there were higher concentrations in the BNL by the second date. At the Mt. Desert Island station, chlorophyll levels were high at the surface and possibly in the BNL.

The only other data for which there were complete profiles are the nanoplankton (Fig. 4) because their abundance can be determined from small water volumes. In Jordan Basin the numbers of autotrophic nanoplankton were much higher at the surface, generally higher on the second sampling date, and possibly elevated in the BNL on the second sampling date. On the other hand, the heterotrophic nanoplankton were more evenly distributed with depth. At the Mt. Desert Island station there was a peak in nanoplankton abundance above the BNL.

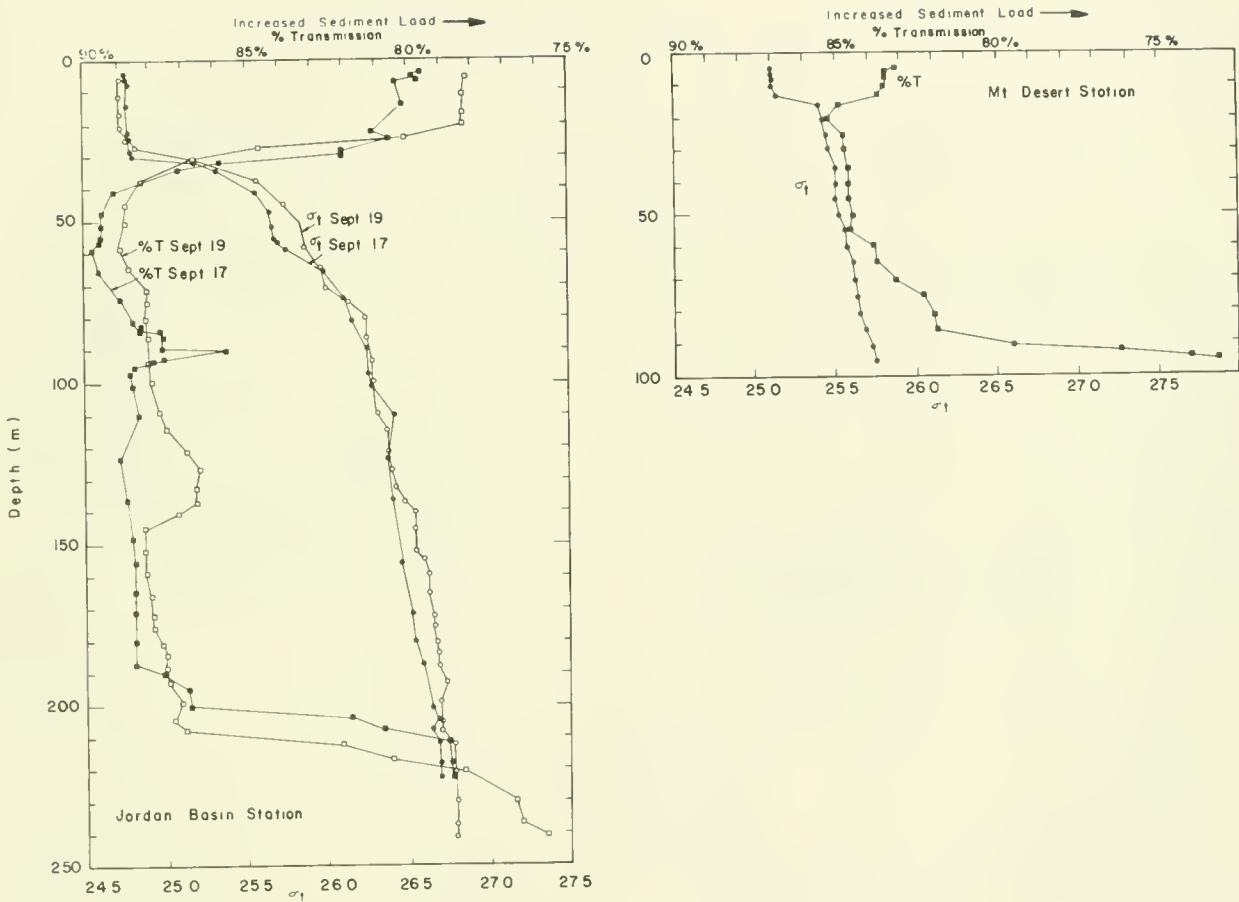


Figure 2. Depth profiles of σ_t and sediment load (% light transmission). Deepest points are 3 meters above the bottom.

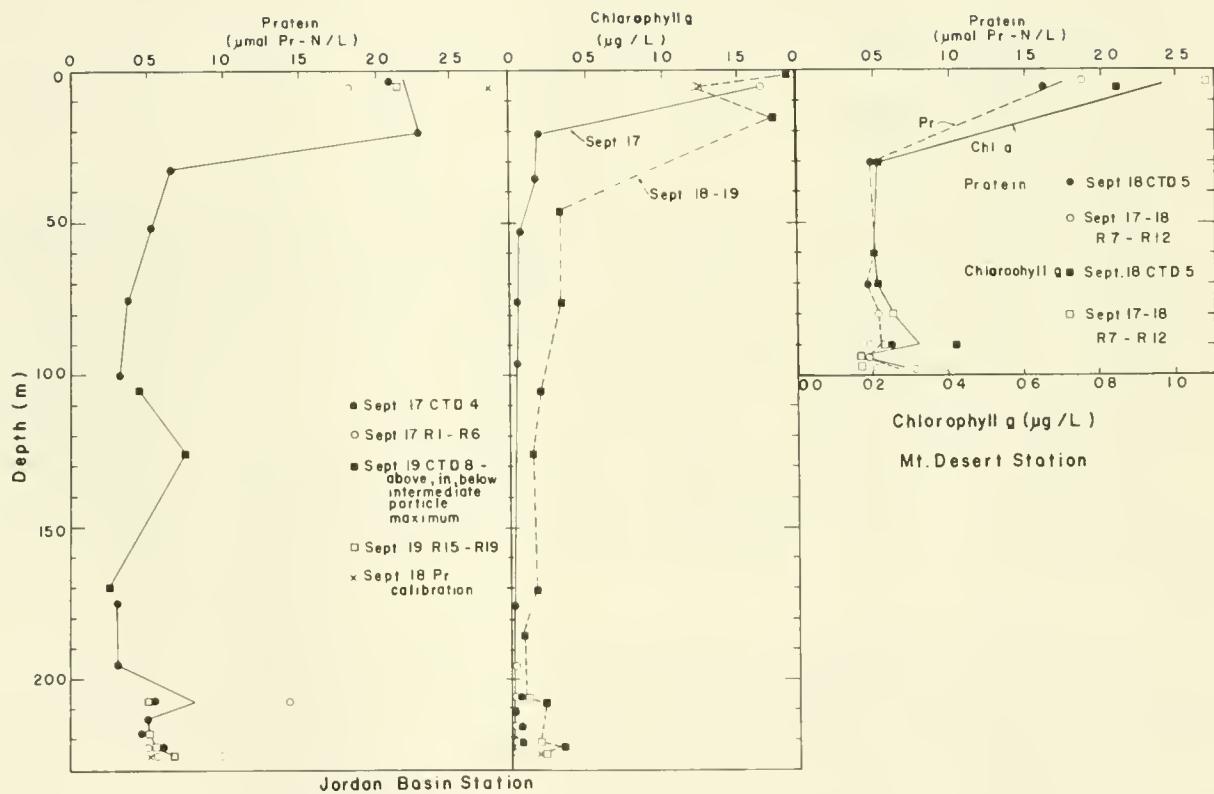


Figure 3. Depth profiles of total protein and chlorophyll *a* concentrations. Deepest points are 2 meters above bottom and bottom depths in BNL at Jordan Basin on later date are adjusted to align depths above bottom for two dates. The points represent individual samples obtained by a variety of sampling methods and on different dates as indicated, lines connect mean values for points at the same depth.

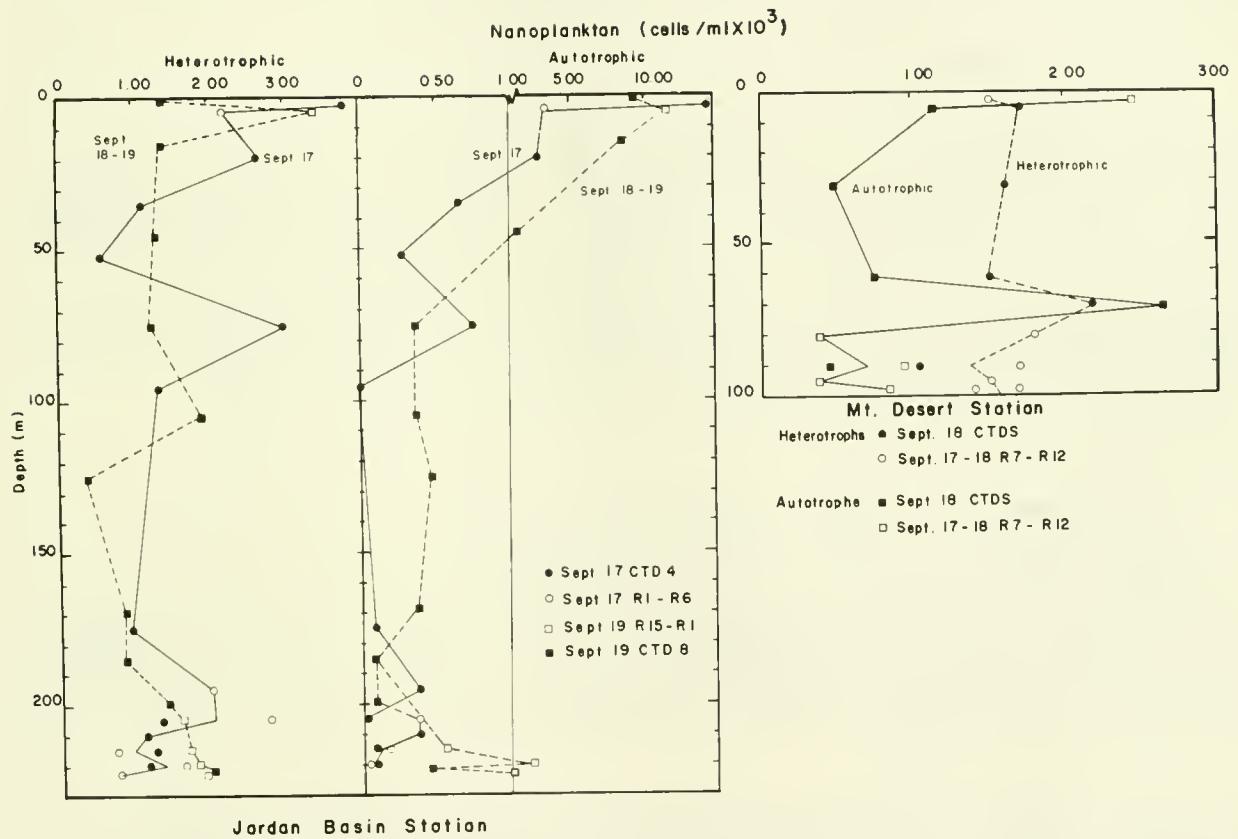


Figure 4. Depth profiles of numbers of autotrophic and heterotrophic nanoplankton (cells/l $\times 10^6$).

Characteristics of Particles in Each Particle Maximum

Surface layer

The surface is the source of particles at depth, although not necessarily directly. It was hypothesized that the surface waters at Mt. Desert Island would be more biologically enhanced, i.e., productive, than the Jordan Basin station because of the proximity to the coast and the hydrography. Although it was suspected that a fall bloom occurred as a result of a storm just prior to sampling in Jordan Basin, there were no significant differences in the characteristics of the particles on the two dates. In the surface layer at Jordan Basin there were significantly higher chlorophyll concentrations and numbers of autotrophic nanoplankton, a greater particle volume, but smaller particles than at Mt. Desert Island. There was no significant difference in protein, ATP or numbers of heterotrophic nanoplankton and not enough data for the other analyses to make comparisons. Because the differences between stations were small, even when significant, all the data reported for the surface layer are means for all dates and times.

Intermediate particle maximum

Most effort went into sampling the BNL, so there is little information about the intermediate particle maximum. It represents a protein maximum (Fig. 3), but not a chlorophyll or nanoplankton maximum (Fig. 3 and 4). Despite the decreased light transmission, the total particle volume was not appreciably different from the water layers above and below, although the slope of the particle size distribution indicates that particles there were much smaller. More information is necessary before this layer can be characterized.

Bottom nepheloid layer

Gradients above the bottom.

The sharp increase in light transmission with distance away from the bottom (Fig. 2) was related to a decrease in the number and volume of particles suspended in the water. It was expected that many of the biological and chemical properties of the BNL would show a similarly steep gradient (Fig. 5-7), but such gradients were rare.

Particulate carbon and nitrogen decreased with distance above the bottom in Jordan Basin (Fig. 5). At both stations some large protozoans either increased (Tintinopsis, Parafavella, foraminifera; Fig. 6) or decreased (Sticholonche; Fig. 6) near the bottom. Finally all stages of copepods tended to be more abundant at 10-20 m than at 2-5 m above the bottom. The lack of a strong gradient in the other measurements could be a result of the sampling method in combination with spatial and temporal variability. The bottom tripping rosette sampled only

one depth approximately every hour and there was considerable variation in replicate samples taken on the same day at the same location (Fig. 2, 3, 5). Gradients may also be more apparent nearer the bottom, but the bottom tripping sampler was not used any closer than 2 m.

In contrast, the BNL in the Sheepscot estuary was sampled with the submersible over a very short period of time and very near the bottom. Except for chlorophyll concentrations, gradients above the bottom were still not very apparent (Fig. 8), suggesting that biological enhancement was not directly related to the amount of suspended sediment.

Comparison of BNL by date and location.

It was hypothesized that the BNL in Jordan Basin would be more biologically enhanced than that at Mt. Desert Island. Before that comparison can be made, the differences in the BNL on the two dates at the Jordan Basin station must be examined, because the chlorophyll and autotrophic nanoplankton profiles (Fig. 3 and 4) suggest some differences between the two dates. There was significantly more autotrophic nanoplankton, chlorophyll, particle volume, copepod eggs and nauplii on the second date than on the first, but many less post-naupliar copepods (Tables 1 and 2). In addition to the differences in concentrations of particles, organisms, and chemical constituents, most indicators suggest that the material on the second date was less degraded (Table 3). There was a

Table 1. Comparison of numbers of organisms in BNL on two dates in Jordan Basin and between Jordan Basin (All) and Mt. Desert Island stations. * indicate pairs of means which were significantly different (Student's 2-tailed t-test, $p \leq 0.05$)

	Date	Bacterial	Nanoplankton ²		Protozoa ³		Copepod ³	
			Auto-	Hetero-	Eggs	Nauplii	Post-nauplii	
Jordan Basin	16& 17	1.69	0.15*	1.33	8540	392*	1763*	897*
	18& 19	1.75	1.00*	1.6	9829	1849*	4301*	192*
	All	1.72*	0.49	1.4	9185	1121	3032	544
	Mt. Desert Isl.	17& 18	3.24*	0.53	1.54	8012	576	3269
¹ $\times 10^8$ cells/L			² $\times 10^6$ cells/L		³ number/m ³			

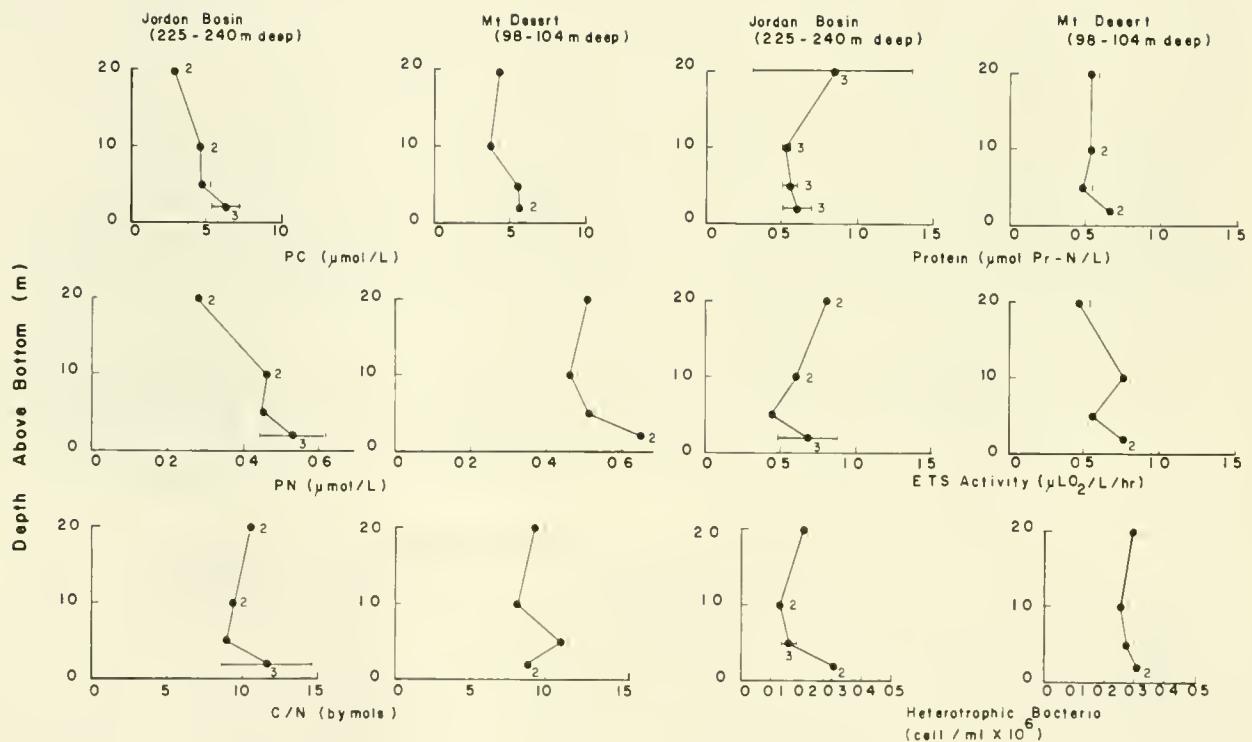


Figure 5. Gradients of particulate C, particulate N, protein, C/N, ETS activity and numbers of heterotrophic bacteria in the BNL. All values are means of all data collected at a particular height above the bottom; small numbers indicate numbers of data points. Error bars are ± 1 standard deviation.

Protozoans $> 35 \mu\text{m}$ in the BNL

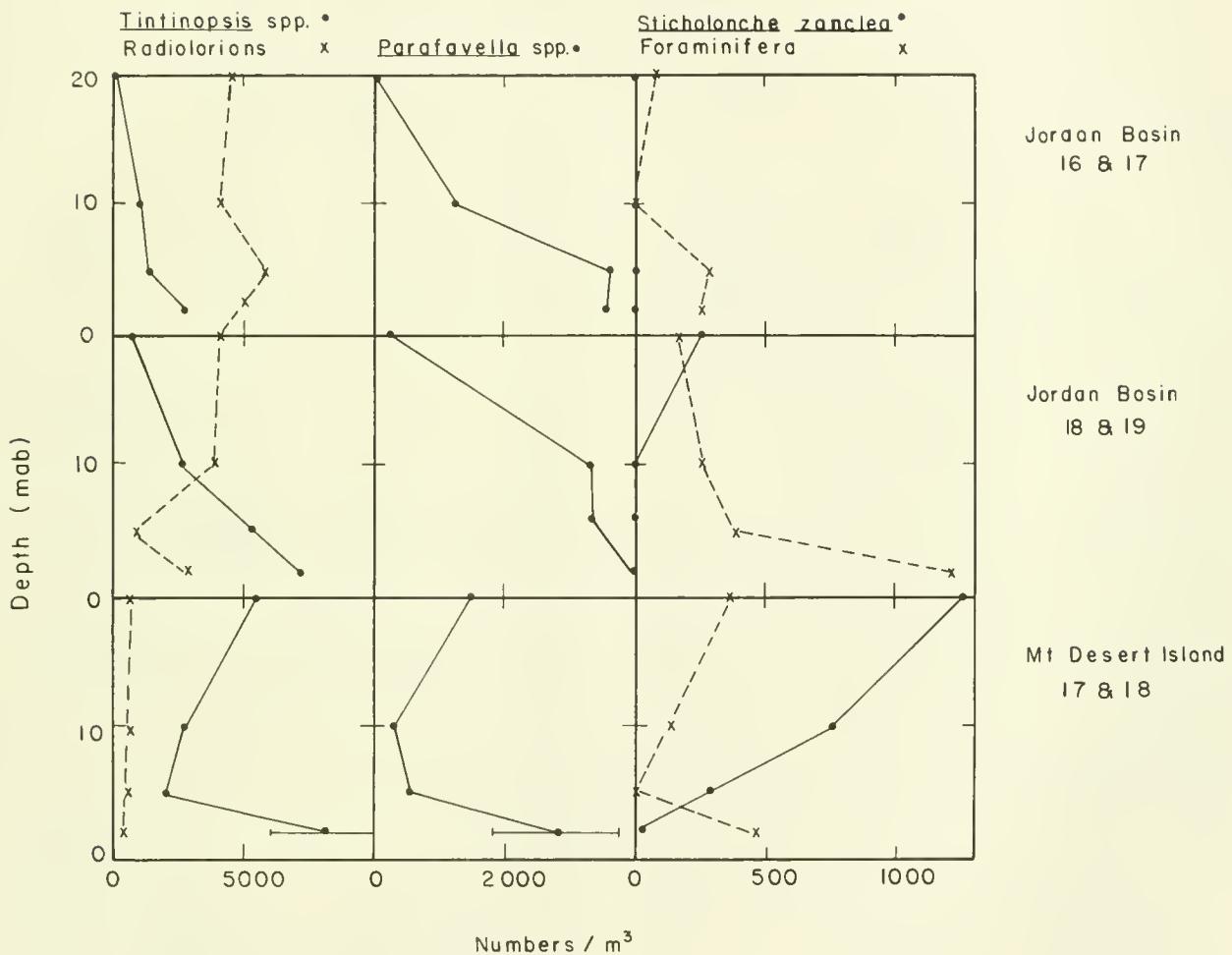


Figure 6. Gradients in numbers of protozoans ($> 35 \mu\text{m}$) in the BNL.

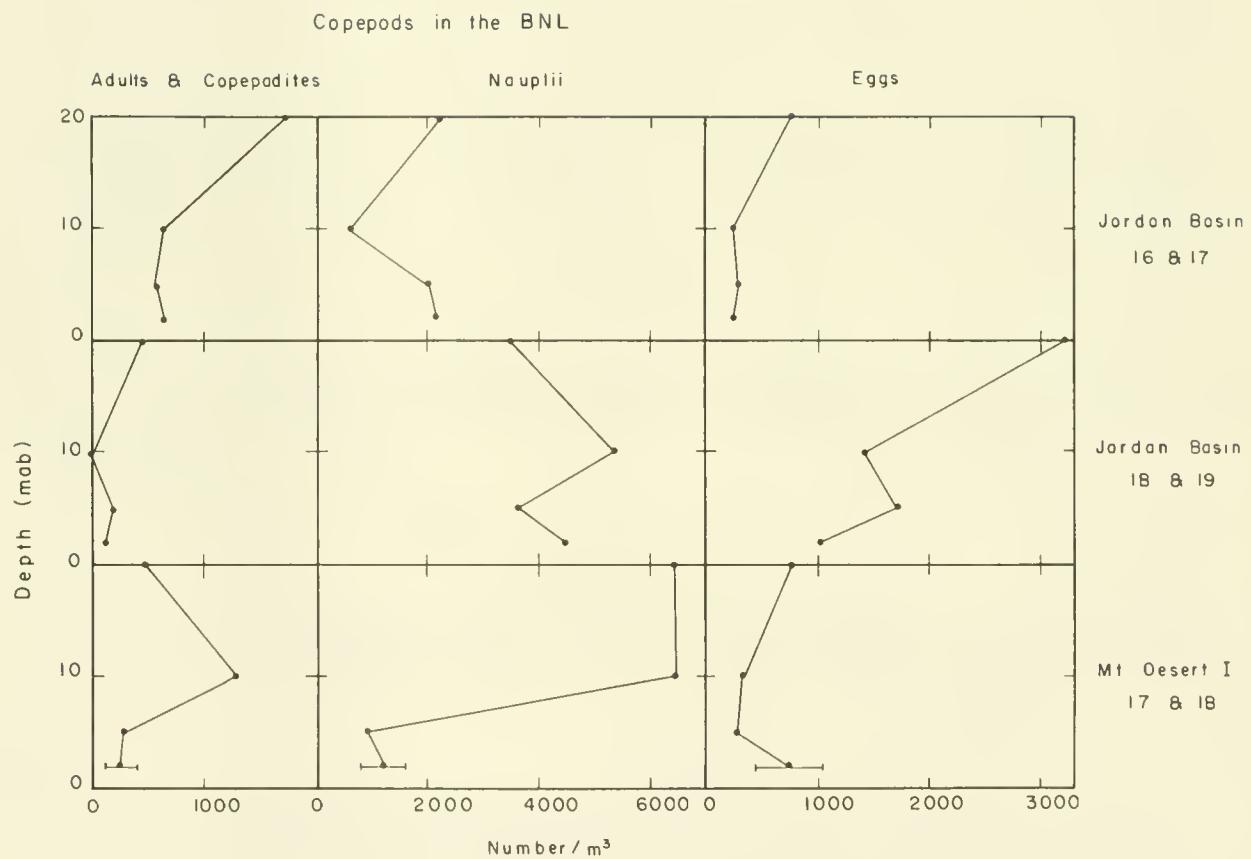


Figure 7. Gradients in numbers of copepods in the BNL.

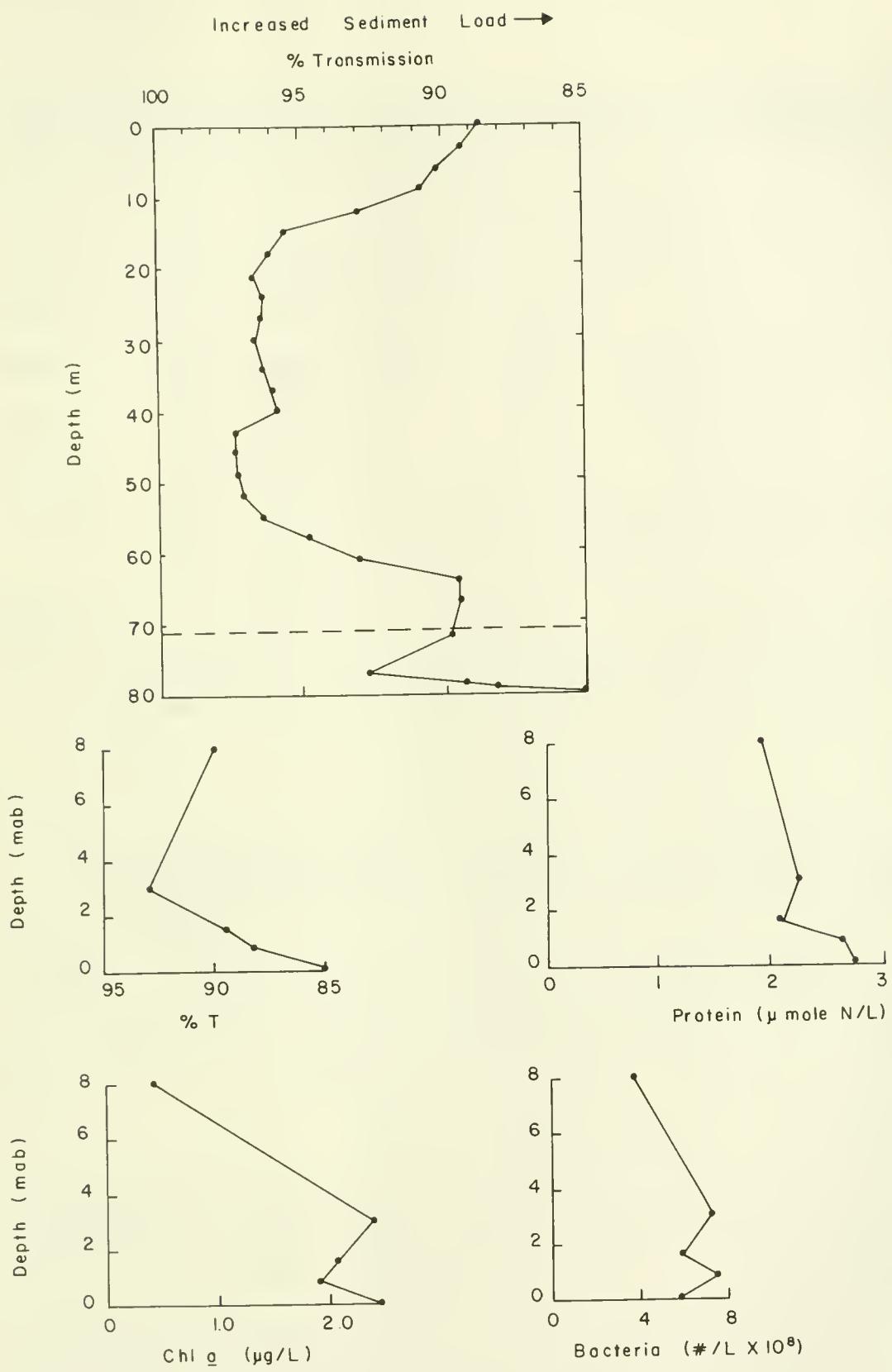


Figure 8. Measurements in the Sheepscot River estuary.

Table 2. Comparison of particle volume and chemical composition in BNL, as in Table 1.

Location	Date	Particle Volume ¹	Protein ²	PC ³	PN ³	ATP ⁴	Chla ⁴
Jordan Basin	16&17	410*	0.69	5.0	0.41	110	0.012*
	18&19	540*	0.57	4.6	0.49	10.9	0.20*
	All	460	0.65	4.8	0.44	60	0.084*
Mt. Desert I	17&18	470	0.57	5.0	0.55	19	0.28*
1ppb	2 μ mol Pr-N/L	3 μ mol/L	4 μ g/L				

significant decrease in the C/N ratio and chlorophyll a made up a higher proportion of both total pigment and total protein biomass. On the other hand, C/ATP ratios were significantly higher on the second date, indicating more detrital carbon. However, C/ATP ratios obtained in this study were generally high, even in the surface layer (Table 6), which suggested a problem with the ATP extraction or analysis.

There were fewer significant differences between the two locations. There were less bacteria (Table 1) and chlorophyll (Table 2) at Jordan Basin. While there was no difference in total protozoa >35 μ m, there were virtually no Sticholonche and many more radiolarians at Jordan Basin (Fig. 6). Higher C/N ratios and lower Chl/Pr ratios at Jordan Basin (Table 3) are indicative of more refractory material with a lower proportion of chlorophyll. Thus, the BNL is less biologically enhanced in Jordan Basin than at Mt. Desert Island, despite the greater enhancement of the surface layer at the station.

Comparisons of the BNL and clear water.

In the description of water column profiles, it was implied that the BNL was biologically enhanced over the clear water just above. There are only a few analyses with enough data for this comparison and the two dates in Jordan Basin must be dealt with separately (Tables 4-6). At the Mt. Desert Island station the only significant difference between the BNL and clearer water was in the volume of particles suspended in the water, which is in accordance with the transmissometry. Thus, the BNL at Mt. Desert Island was not biologically enhanced over the clearer water. At the Jordan Basin station the particle volume, protein concentrations, and Chl/protein ratios were always higher in the BNL. On at least one date the numbers of autotrophic nanoplankton were higher, the % of undegraded chlorophyll a was

lower and the particle sizes were smaller in the BNL. Thus there was some evidence that the particles in the BNL at Jordan Basin were different from those in the clearer water above and that they were biologically enhanced.

Table 3. Comparison of indicators and rate measurements in BNL, as in Table 1.

Location	Date	C/ ATP ¹	Pr/ PN ²	C/N ³	Chl/ Pr ⁴	Chla/ Total Pigment ⁵	Resp. ETS ⁶	Slope	Size Distribution
Jordan Basin	16&17	2120*	230	11.9*	0.174*	12.6*	0.77	3.21	
	18&19	5600*	129	9.6*	0.64	44.0*	0.51	3.18	
	A11	3400	190	11.0*	0.33*	25.0	0.65	3.2	
Mt. Desert I	17&18	4300	101.0		9.1*	1.32*	36.0	0.663.0	
1by wt	2% mole N	3by mole	4u g/u mole N	5% by wt	6u LO ₂ /L/hr				

Table 4. Comparison of numbers of organisms between BNL, clear and surface water. * indicate pairs of means which are significantly different (Student's 2-tailed t-test, p ≤ 0.05).

Location	Date	Layer	Nanoplankton ¹	
			Autotrophic	Heterotrophic
Jordan Basin	16&17	BNL	0.15	1.33
		Clear	0.36	1.49
	18&19	BNL	1.0*	1.6
		Clear	0.30*	1.14
Mt. Desert I	17&18	BNL	0.53	1.54
		Clear	1.30	1.77
Both	16-19	Surface	6.4	2.27

1 x10⁶ cells/L

Table 5. Comparison of particle characteristics between BNL, clear and surface water, as in Table 4.

Location	Date	Layer	Chemical Chl a ¹	Composition Protein ²	Particle Volume ³
Jordan Basin	16&17	BNL	0.12	0.69*	406*
		Clear	0.055	0.417*	135
	18&19	BNL	0.20	0.572*	544*
		Clear	0.20	0.369*	230*
Mt. Desert I	17&18	BNL	0.28	0.57	470*
		Clear	0.20	0.47	272*
Both	16-19	Surface	1.08	2.09	610
1 <u>u</u> g/L	2 <u>u</u> mole Pr-N/L	3ppb			

Table 6. Comparisons of indicators between BNL, clear and surface water, as in Table 4.

Location	Date	Layer	Chl a/ Total Pigment ¹	Chl/ Protein ²	Slope Size Distribution
Jordan Basin	16&17	BNL	12.6*	0.180*	3.21
		Clear	25.8*	0.40*	3.04
	18&19	BNL	44.0	0.645*	3.18*
		Clear	41.0	1.32*	2.82*
Mt. Desert I	17&18	BNL	36.0	1.32	3.0
		Clear	38.9	1.12	3.13
Both	16-19	Surface	47.5	1.09	3.28
1% by wt	2 <u>u</u> g/u mole Pr-N				

Biologically Available Protein

Although the BNL is enhanced in total protein, measurements of biologically available protein, i.e., that readily degraded by proteases, show that a much smaller fraction of the total protein may be utilized by organisms in the BNL than in the surface layer (Table 7). The remaining "protein" may be tied up in humic material or an artifact of using the Lowry method in the presence of humic materials.

Table 7. Concentrations of total and biologically available protein at Jordan Basin.

Depth (m)	Total Protein ¹	Available Protein ¹	% Available
2 above bottom	0.53	0.11	21
5 from surface	2.76	2.31	84

¹u mole Pr-N/L

DISCUSSION

In summary, three particle maxima were observed at Jordan Basin and two at Mt. Desert Island. The surface layer at Jordan Basin had higher chlorophyll concentrations, autotrophic nanoplankton numbers, and particle volumes than the Mt. Desert Island station, but other analyses indicated no significant differences. An intermediate particle maximum was observed at Jordan Basin which was enhanced in protein, but not other constituents. The BNL, which was characterized by a sharp gradient in light transmission and particle volume, did not show gradients in most of the biological or chemical constituents, except some protozoans. Considerable temporal/spatial variability was apparent in the BNL for replicates obtained within a short time, which may obscure gradients. The BNL at the Jordan Basin station was less biologically enhanced than the Mt. Desert Island station and the organic material appeared to be more degraded. Nevertheless, the BNL at Jordan Basin was more biologically enhanced over the clear water above than at the Mt. Desert Island station, probably because the clear water at Jordan Basin was much clearer than at Mt. Desert Island (Fig. 2). Finally, there were differences at all depths, but especially in the BNL, between the two sampling dates at Jordan Basin. The data cannot be used to distinguish between two alternate explanations: a fall bloom occurred in response to a storm and the material was transported vertically or horizontal advection patchiness changed the characteristics of the water and particles at the one location. In conclusion, there was some evidence that the BNL at some stations in the Gulf of Maine was biologically enhanced, and could, thus, serve as a food source for benthic organisms and demersal fishes.

While it seems to be generally agreed that BNL are biologically enhanced (e.g., Karl et al., 1976; Rowe and Gardner, 1979; Wishner, 1980 a, b.; Angel and Baker, 1982; Smith, 1982; Kawana and Tanimoto, 1984; Wishner and Meise-Munns, 1984; Gowing

and Wishner, 1986; Noriki and Tsunagai, 1986; Wishner and Gowing, 1987), it is technically difficult to conduct detailed sampling in the BNL in order to examine horizontal, vertical, and temporal variability. The data presented here and in Smith et al. (1987) and Wishner and Gowing (1987) suggest considerable spatial/temporal variability in the biological and chemical constituents. Some of the variability between the stations can be related to differences in hydrography and environmental conditions at the two stations, i.e., the Mt. Desert Island station is shallower, well mixed and has strong bottom currents. The differences in the BNL between the two dates at Jordan Basin could have been related to the occurrence of a fall bloom or horizontal movement of patches. But the variation between replicates taken within a short time and the lack of strong gradients in biological and chemical measurements suggests that processes in the BNL are quite complex. For example, the lack of strong gradients could result because organically-enriched, nutritionally-enhanced particles may be finer and suspended at greater heights above the bottom than the rest of the larger sediment grains (Muschenheim, 1987). Accordingly, in our study copepod numbers appeared to be higher at the top of the BNL than at the bottom.

Understanding the dynamic processes affecting the nutritional quality, distribution of variables in general, and mechanisms of formation of BNL will require technically sophisticated sampling devices, probably deployed with a submersible. It is necessary to sample very near the bottom and to be able to take samples in the BNL and the overlying clearer water simultaneously.

Because the flux of organic material to the bottom is greatest just after the spring bloom, the BNL in the spring and early summer should be much more biologically enhanced than in the late summer and fall periods reported here. Finally, more physical measurements and more definitive methods of assessing nutritional value and biological activity are necessary for understanding dynamics in the BNL. In our 1987 field program in the Gulf of Maine we were able to improve the sampling capability through the use of the Johnson Sea-Link. Although some technical problems remain, the methods of assessing biological enhancement were improved. These results will be reported in the near future.

ACKNOWLEDGEMENTS

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EPIBENTHIC KRILL IMPACT PARTICLE AND FOOD WEBS:
DETECTION BY SUBMERSIBLE

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ABSTRACT

Recently, submersible dives in the Gulf of Maine and the canyons south of Georges Bank revealed that prodigious numbers of fecal pellets ($200-350 \text{ particles} \cdot \text{m}^{-3}$) accumulated at night in 5-17 m thick layers coincident with the pycnocline (15-30 m). These large, cylindrical (0.2 mm OD x 3-5 mm long) particles sank rapidly ($200 \text{ m} \cdot \text{d}^{-1} \pm 25 \text{ SE}$) and could-transport substantial amounts of organic matter ($35 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) to the bottom. Vertically migrating euphausiids *Meganyctiphanes norvegica* produced the pellets after feeding in the mixed layer. These individuals represented only part of enormous ($10^2-10^4 \text{ individuals} \cdot \text{m}^{-3}$) aggregations of adults (25-35 mm long) which remained within 10 m of the seabed day and night and appeared to forage in the benthic boundary region. These discoveries are significant because they improve our basic understanding about the dependence of benthic communities on zooplankton grazing in the mixed layer and expose variability in diel migratory and feeding behaviors of a single zooplankton species, concomitantly indicating the existence of unquantified pathways of particle transport. Furthermore, the unexpected observations of such large, epibenthic stocks of krill disclose the location of major food resources that have probably supported the centuries-old fishery in this region.

INTRODUCTION

In general, the amount of particulate matter in the oceans decreases exponentially below the productive photic zone (Hargrave, 1984). The relatively rapid ($1-1000 \text{ m} \cdot \text{d}^{-1}$) sinking of heavy particles like zooplankton fecal pellets can contribute substantially to the vertical export of organic compounds and various elements (Fowler and Knauer, 1986). However, the amount of fecal matter produced and the rate at which this matter settles vary considerably in relation to a host of physical and biological factors, e.g., advection, viscosity, diet, and decomposition. Consequently, mathematical models developed to predict regional and global flux rates of biogenic material require detailed information about the production and distribution of these important particles (Hargrave, 1985). Most of the existing data about particle flux has been based on in situ sampling with sediment traps, pump-supported equipment, optical techniques or scuba (Alldredge and Gotschalk, in press,; Bishop et al., 1985; Lampitt, 1985; Urrere and Knauer, 1981). Data obtained from sediment traps and optical-based devices can be misleading in that the amount of material measured may be a mixture of particles from vertical sinking, lateral advection and resuspension. Similarly, information derived from filtration systems may include both suspended and fast-sinking particles. Scuba assessments of the sizes, sources and sinking of particulate material are depth limited.

We report here another approach, the use of a technically advanced, manned submersible. Our water column research showed where and when fecal pellets were produced by the euphausiid Meganyctiphanes norvegica and quantified the chemical composition and flux of these biogenic particles. The persistence of feeding activity in both mixed layer and epibenthic regimes by large populations of euphausiids was unexpected and introduces, via egested feces, a substantive supply of utilizable food for demersal suspension- and deposit-feeding invertebrates.

METHODS

Fecal pellets and euphausiids were observed in situ with the Johnson Sea-Link submersibles within the Gulf of Maine and along the southern edge of Georges Bank during July-August in 1983, 1984 and 1985 (Fig. 1). Devices designed to collect fecal pellets for chemical and other measurements were available only in 1985. Vertical depth profiles of temperature, conductivity and transmittance were recorded simultaneously at 1-s intervals with a data logging system attached to the submersible (Youngbluth, 1984).

One or more of four techniques, two photographic, one visual and one collection, were used to quantify the abundance of fecal pellets and euphausiids in the water column. The first method employed a 70 mm Hasselblad camera/strobe configuration to take color images of approximately 0.004 m^3 of seawater directly

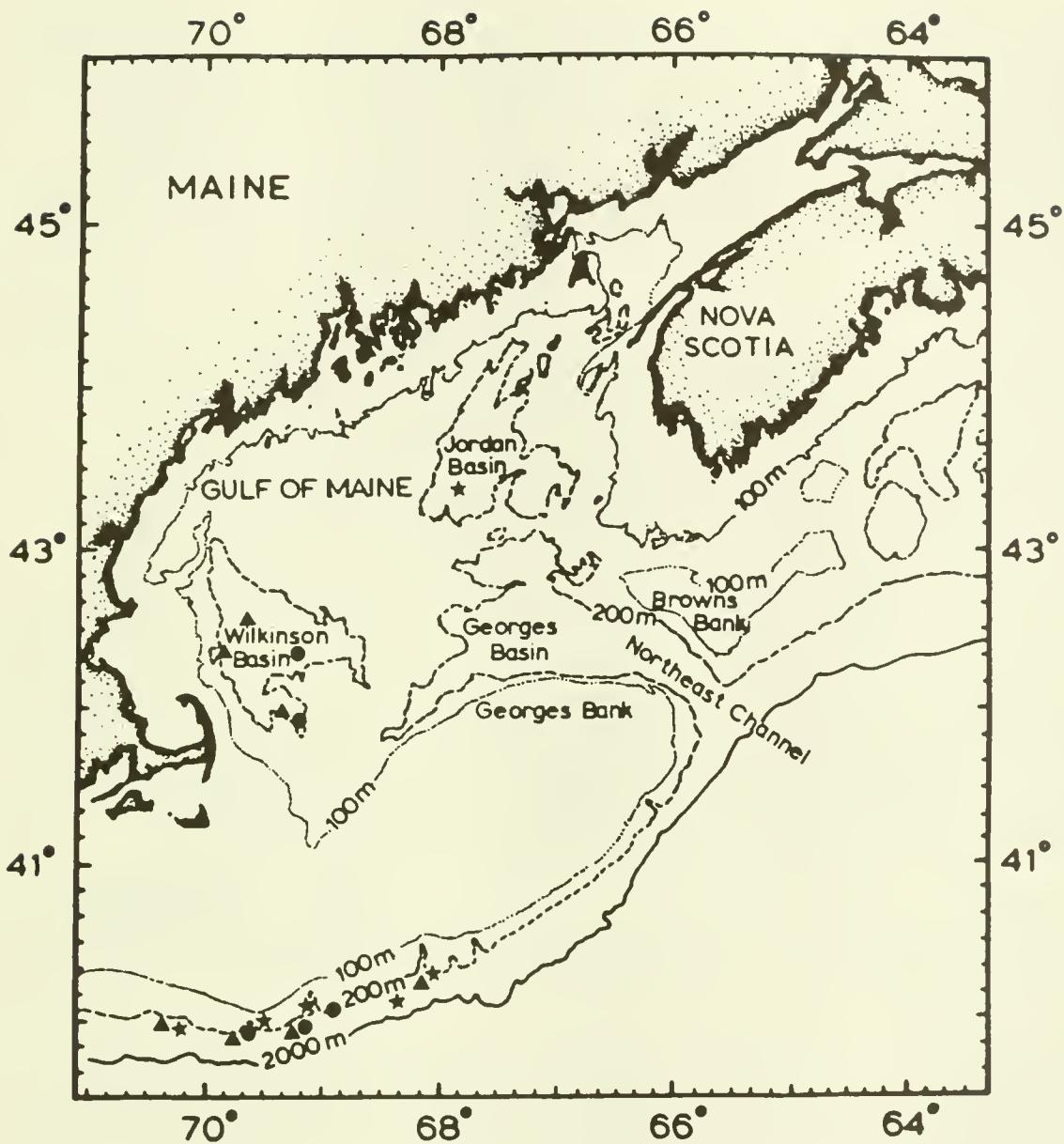


Fig. 1. Locations of submersible dive sites where epibenthic aggregations of the euphausiid *Meganyctiphanes norvegica* were observed, photographed or collected. (circle) 10-17 July 1983, (star) 9-19 August 1984, (triangle) 1-6 July 1985. Bottom depths ranged from 200-800 m.

forward of the submersible's acrylic pressure hull. The second system consisted of a 35 mm Benthos camera/fresnel lens package (Honjo et al., 1984) to take black-and-white photographs of a light-defined volume (0.28 m^3) at 12-s intervals while the submersible moved horizontally at 0.7 kt for 5-min transects. Abundances were also estimated *in situ* by visual observations using nearest neighbor distances (Mackie and Mills, 1983). Care was taken to limit the use of submersible lights when estimating krill abundance.

Fecal pellets were collected using eight specially-designed cylindrical 7.5 l acrylic samplers (17.6 cm ID x 35.4 cm long). These samplers were mounted vertically along a linear framework just forward of the submersible's pressure hull. The ends of each cylinder were sealed by a pair of lids that moved horizontally over the openings. Sieves consisting of 209 μm plankton netting glued to 8 cm tall, acrylic frames (17 cm ID) were inserted into the bottom of each sampler. In use, the samplers' lids were partially opened during launching of the submersible. After launch, as soon as the samplers filled with water forcing out all residual air, the lids were closed. The submersible then descended to a depth just below the layer of fecal pellets, the lids were opened and the submersible was made just slightly positively buoyant. After traversing upwards through the fecal pellet layer, the lids were closed, and the submersible descended again to just below the layer where the sampling process was repeated five to six times. The total volume filtered by each sampler ranged from 1-1.5 m^3 .

Sinking rates (Komar et al., 1981) of fresh, individual pellets were measured at several *in situ* temperatures onboard ship using a gimballed, cylindrical glass container (46 cm tall x 6 cm ID) filled with filtered (0.4 μm) seawater.

Microbial enumerations followed established procedures (Davoll and Silver, 1986). Fixation techniques for scanning electron microscopy were standard (Blades and Youngbluth, 1979). Proximate chemical analyses employed proven methods (Bailey and Robison, 1986).

RESULTS

At most locations, pellets occurred in a discrete layer (ca. 5-17 m in vertical extent) between midnight and sunrise. The bulk of these layers coincided with the pycnocline (Fig. 2). By mid-morning such concentrations were absent at the density interface, but pellets were still conspicuous, although quite dispersed, throughout the deeper Maine Intermediate Water.

Fecal pellet abundance within the layers averaged $325 \text{ pellets} \cdot \text{m}^{-3} \pm 29 \text{ SE}$. The pellets were relatively large, cylindrical rods (0.2 mm OD x 3-10 mm long) and golden-brown in color. Both the vertical distribution and relative abundance of fecal pellets coincided with the presence of the euphausiid

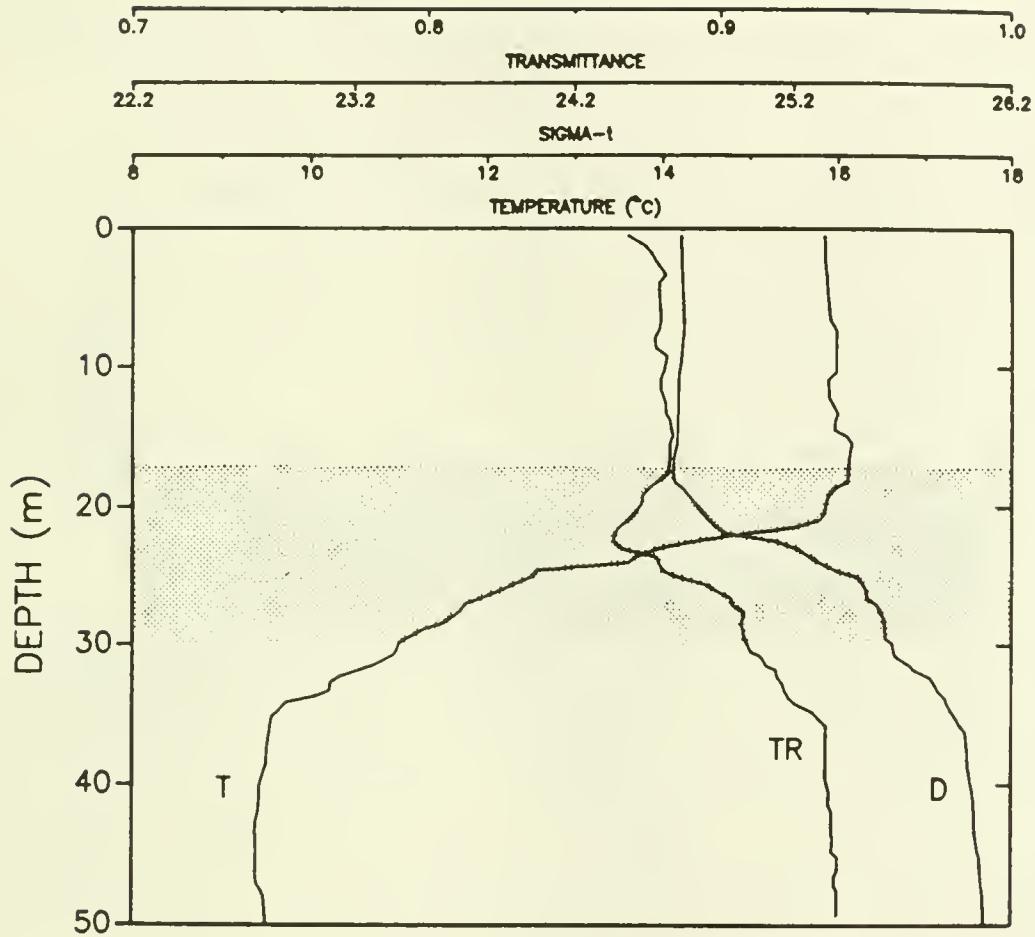


Fig. 2. Example of the accumulation ($300 \cdot m^{-3}$ within the stippled area) of euphausiid fecal pellets near the pycnocline. Dive 1107, $40^{\circ}21.55' N$. Latitude, $68^{\circ}08.86' W$. Longitude, 4 July 1985.

Meganyctiphanes norvegica

Settling velocities of pellets, measured under shipboard laboratory conditions and integrated to account for physical/chemical differences throughout the water column, averaged $8.3 \text{ m} \cdot \text{h}^{-1} \pm 1.2 \text{ SE}$ which indicated that pellets produced near the sea surface could settle to the deep basins in the Gulf of Maine at 240 m in about one day (29-h). If all of the pellets collected near the pycnocline were to reach the sea floor, the accumulated abundance would be $5000 \text{ pellets} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.

Fluorescence microscopy indicated that the fecal material contained a variety of microbial populations. The major live microbes, their abundance (cells \cdot pellets $^{-1}$) and enrichment above background seawater concentrations were $<10 \text{ u m}$ eucaryotic autotrophs (1.3×10^{-3} , 9200X), coccoid cyanobacteria (7.5×10^{-4} , 20,000X) and heterotrophic bacteria (1.2×10^{-5} , 1200X). Living microbial carbon, however, accounted for only 0.1% of the average fecal carbon content ($2.6 + 0.6 \text{ SE ug C} \cdot \text{pellet}^{-1}$). Scanning electron microscopy of the pellets showed only a few recognizable phytoplankton tests and zooplankton exoskeletons interspersed among masses of unidentifiable amorphous, granular matter. These data were consistent with proximate chemical analysis which revealed the feces to be high in ash content (76% dry weight, DW) and low in organic components (protein=4.5% DW, lipid=0.4% DW, carbohydrate=2.1% DW). Carbon and nitrogen values (C=5.1% DW, N=0.9% DW) produced a high C:N ratio of 5.7.

DISCUSSION

In spite of the low organic content, this single source of fecal material could supply $35 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ to the benthic community. This biomass represented 20% of the daily primary production in the mixed layer (Townsend and Cammen, 1985). If oxidized completely, the fecal material would yield an oxygen consumption rate of $10 \text{ ml O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, i.e., at least 8% of the total benthic community respiration (Smith and Hinga, 1983).

Assuming a gut evacuation rate of 1 - 2 h and a daily grazing cycle of 8 h in the mixed layer (Willason and Cox, 1986; Heyraud, 1979), about $7 - 68 \text{ euphausiids} \cdot \text{m}^{-3}$ could have produced the number of pellets observed near the pycnocline. This conservative estimate of population abundance supported our visual observations that in most cases only a small portion of the euphausiids, which aggregated near the bottom, actually migrated upward at night into the mixed layer. Furthermore, the deep-living cohorts in the benthic boundary region usually had full stomachs and appeared to be foraging when observed, i.e., feeding on particulate material in the epibenthic nepheloid layer and possibly on the flocculent "fluff" layer at the sediment-water interface.

These direct observations of *Meganyctiphanes norvegica* support previous trawl-based investigations of the distribution

and feeding patterns presumed to occur in the western North Atlantic and Mediterranean seas (Mauchline, 1980; Bigelow, 1927). However, whether or not a diet solely of detrital material can meet the metabolic needs of this species requires further study (McClatchie, 1985). If consumption of detritus in the epibenthic region can be quantified, these euphausiids constitute a huge, heretofore unidentified grazing force which may account for considerable repackaging and bioturbation. Assuming that epibenthic *M. norvegica* feed more or less continuously, those individuals that migrate vertically each night may introduce recycled biogenic and inorganic materials back into the mixed layer when they release fecal pellets.

The detection of prodigious epibenthic aggregations of euphausiids is also significant in regard to higher trophic level dynamics throughout the region studied. For example, marine carnivores such as fin-whales (*Balaenoptera physalus*) are known to feed almost exclusively on euphausiids, presumably on patches of high (at least $17 \text{ g} \cdot \text{m}^{-3}$, ca. $60 \text{ individuals} \cdot \text{m}^{-3}$) biomass (Brodie et al., 1978). Unpublished data from the Marine Monitoring Assessment and Prediction Program (MARMAP) have indicated that euphausiid densities in the study area average less than $1 \cdot \text{m}^{-3}$ and range up to 50. Sonar (120 kHz) measured densities of 5-140 euphausiids $\cdot \text{m}^{-3}$ (Sameoto 1983). Our observations that epibenthic krill were at least one to two orders of magnitude higher than mean abundances recorded by net tows or sonar measurements, substantiate that zooplankton do occur in concentrations that can supply daily food rations required by these mammals. We and other scientists (P. Auster, R. Cooper, R. Jones, R. Langton, J. Uzmann, pers. comm.) have seen demersal fishes (*Gadus morhua*, *Pollachius virens*, *Merluccius bilinearis*, *M. albidus*, *Urophycis tenuis*, *U. chuss*) and squids (*Loligo pealei* and *Illex illecebrosus*) feeding on epibenthic populations of euphausiids. These preliminary observations of foraging by cod, hake, pollock and squid weaken the hypothesis that these zooplankton may avoid predation by living near the bottom and support fisheries data that indicate *Meganyctiphanes norvegica* is an important food resource for commercial groundfish species (Grosslein and Azarowitz, 1984). Consequently, by virtue of enormous densities, daily migrations, and widespread distribution in nearshore waters, populations of *M. norvegica* probably impact benthic productivity over a broad geographic area in the North Atlantic Ocean in at least three ways: (i) as sources of biogenic particles (fecal pellets, molts and carcasses), (ii) as bioturbators and transporters of resuspended and flocculent sediments and (iii) as prey for demersal predators.

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DESIGN AND FABRICATION OF A FLUFF LAYER SAMPLER

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ABSTRACT

Organic-rich detritus from spring blooms settles to the sediments to form an organic-rich layer, which has not been properly sampled to date. We present here a description of a fluff layer sampler (FLS) which can obtain this material by using a carefully controlled resuspension followed by in situ filtration. The resuspension takes place in a flume nozzle carefully emplaced at the sediment-water interface, with a bottom friction velocity (u^*) of about 0.4 cm/sec. The resuspended material is pumped through a glass fiber filter for return to the surface. This device may be deployed by a SCUBA diver or submersible, using either an independent lander containing its own pump and filter apparatus, or pump and filter apparatus provided by the submersible (e.g., Johnson Sea-Link).

INTRODUCTION

A significant fraction of ecosystem metabolism in coastal and continental shelf systems occurs in the sediments. A number of studies of this sediment metabolism have pinpointed the sediment-water interface as a particularly important zone (e.g. Reimers and Suess, 1983; Silverberg et al., 1985). In temperate zones, a significant to major fraction of organic matter input to the sediments occurs as a result of settling of the spring bloom, as a result of inefficient zooplankton grazing in the springtime before stratification and warming take place. While this organic input has been inferred from time-series sediment trap studies (e.g., Smetacek, 1980; Wassmann, 1984; Davies and Payne, 1984), the emplaced organic matter lying on the surface of the sediments has not been properly sampled to date. Actual observations of the material are noted only in anecdotal and occasional time-series bottom photo studies (e.g., Lampitt, 1985). Attempts to sample this material do not generally result in material that is dominantly organic (e.g., Christensen and Kanneworff, 1986).

The inability to sample this very important material derives from its very loose and biochemically labile character. Its residence time as a layer distinctly on top of the sediments is likely on the order of days to weeks (Lampitt, 1985) before it is either metabolized or transported away by bottom currents to redeposit in lower energy depositional sites. The physical looseness of the material has earned for it the names "fluff" or "flocculant" layer. As the latter term connotes an aggregation process that is not yet demonstrated, the former term - fluff layer - will be used here.

The physical looseness of the material renders its sampling quite difficult. Most benthic sampling devices deployed from a ship create a severe bow wave during descent, and consequently push aside this material before entering the sediment. Attempts to sample from a ship generally involve, therefore, an insertion of a coring device done as slowly as possible. Upon retrieval, the approach is generally to either scrape as fine a layer of material from the sediment-water interface as possible, or to induce a gentle resuspension of the fluffy material by agitating supernatant water left in the coring device.

In this paper we describe an approach to the sampling of this layer that relies on (1) an in situ visit to the sediment-water interface by submersible or SCUBA diver, and (2) a flume device that relies on the physical looseness of the fluff layer to resuspend it without resuspending the underlying sediment.

This paper will focus only on the design and technology of deployment of a fluff layer sampler (FLS). Our first submersible dives were carried out in the months preceding this Symposium, and the scientific results from these dives are not yet ready for publication.

DESIGN AND FABRICATION OF THE FLS

Design rationale

We have chosen to build a sampler that collects the fluff layer by a carefully controlled water flow over the sediment-water interface, such that only the fluff layer is resuspended. The flow is generated in a short flume nozzle by drawing water through an open end and withdrawing it to a filter assembly where it is collected on a glass fiber filter. The collection is designed to provide enough material to undergo analyses for carbon, nitrogen, and labile protein concentrations, in order to test the hypothesis that the fluff layer is a zone of nutritionally enriched material relative to the underlying sediment.

A substantial literature exists on the water motion required to resuspend marine sediments (reviewed in Nowell et al., 1981), but there are very few published data on the fluid flow capable of resuspending fluff layers. The water flow necessary to resuspend sediments is usually parameterized at the critical shear velocity (sometimes called friction velocity or critical entrainment velocity), and is given by the expression -

$$u^* = (\tau/\rho)^{1/2}$$

where u^* is the critical shear velocity, τ is the critical shear stress, and ρ is the water viscosity. The u^* parameter has units of velocity (e.g., cm/sec) but does not actually represent a velocity. Depending on the topography of the bottom sediment, its value is often on the order of 1/25 of the bottom current at an elevation of a meter or more above the sediment-water interface. The critical shear velocities necessary to resuspend marine bottom sediments are usually >0.8 cm/sec. (Nowell et al., 1981). The only published literature that allows estimation of the u^* necessary to resuspend the fluff layer is from the combined bottom photo and current meter time series of Lampitt (1985), which results in a critical u^* of about 0.3 cm/sec.

We chose a u^* of 0.4 cm/sec as an operating shear velocity at which to run the flume. The fluff layer therefore takes on an operational definition based on its susceptibility to erosion, rather than a depth definition or a non-quantifiable type of resuspension such as might be done in a box core.

The size of the flume was dictated by the sample requirements on which we can conduct the protein and C/N analyses - about a gram of fluff layer material. As a conservative calculation, assume a fluff layer thickness of 2 mm consisting of material with a water content of 98% and a solids' density of about 1.0 g/cm³. The flume's floor (19.9 cm x 14.2 cm) has an area of 283 cm², which is sufficient to produce the required gram of material with these conservative assumptions.

The inverted flume nozzle (Figure 1) was designed with the goal of achieving a homogeneous shear velocity field over the entire confined sediment area. A trip bar at the opening of the flume creates a controlled stress distribution at the beginning of the flow. In a square duct aligned horizontally, a boundary layer flow would then develop with the u^* prescribed by laminar or turbulent bottom stress formulae, depending on the Reynolds number. This u^* would vary with downstream distance. The top wall of the flume nozzle was angled to preserve the desired u^* distribution over the length of the flume. The optimal angle of this top wall was determined in an experimental program using skin friction sensors (Gust, submitted) and a pumping rate of 22.9 l/min. This experimental work was performed in a laboratory recirculating flume, with flow through the flume nozzle provided by an aquarium pump. The skin friction sensor was mounted flush with the bottom of the larger recirculating



Figure 1. Photograph of flume nozzle.

flume, and the flow field in the flume nozzle determined by moving it relative to the skin sensor. The u^* field with a flow of 22.9 l/min is shown in Figure 2. The subsequent field-deployable flume nozzles were built using Plexiglas, with vertically extended sidewalls to penetrate into the sediment.

The resuspended fluff layer material flows through six holes at the end of the flume and is withdrawn to flow through a filter assembly. There are two configurations for this "downstream" pumping filtering assembly.

The configuration for the Johnson Sea-Link mounts the flume on its hydraulic arm, and utilizes its pump capability, operated by the hydraulic system, and a filter holder assembly designed by Dr. D. Long (Michigan State University). The pump is located downstream of the filter holder, with a flow meter to provide the cockpit crew with instantaneous flow rate and accumulated flow information. The filter holders, constructed of aluminum, hold filters of 19.8 cm diameter, and are placed in a bucket mounted on the sub's lazy susan array. At the time of this writing, the sub has the capability for only one filter usage per dive. While the lazy susan array normally allows for multiple bucket usage, the weight of the filter holder prevents the normal tight fit between the upper edge of the bucket and the top plate overlaying the buckets, which is necessary to ensure that (1) pumped water does not leak out of the bucket before going through the filter, and (2) entrainment of outside water occurs into the slurry containing the fluff material. A filter placed into another bucket for the duration of a dive serves as a control for processes such as adsorption of dissolved organic matter onto the filter. We use Schleicher and Schuell No. 30 glass fiber filters, which have acceptable flow rate and an effective pore size of several micrometers.

The Delta submersible does not provide pumping and filtration capability, and thus requires a completely self-contained unit. Accordingly, we have built a lander device containing all of these functions, which can be deployed by either submersible or SCUBA divers (Figure 3). This device consists of a housing containing power supply, motor, pump and control circuitry carried on two skids, between which is mounted the sampling flume. The housing was fabricated from 6061 (T6) aluminum pipe, 36" long x 8" dia. x 0.375" wall thickness, with 3/4" end plates, welded at one end, flanged, O-ringed and bolted at the other, with the entire assembly anodized. Inside the house a 24 volt battery pack (12 sealed, starved electrolyte cells) is contained inside a separate gas-tight aluminum housing. The batteries are connected, through a magnetically activated reed switch attached to the inside wall of the housing, to a 24 volt, 5 amp, 3600 rpm motor. This motor drives through a specially-designed magnetic coupling to a nylon centrifugal pump mounted on the outside of the flanged end wall of the housing.

The pump was operated by holding a magnet next to a target

0.19	0.24	0.22	0.43	0.42	
0.60	0.49	0.38	0.37	0.29	→
0.58	0.42	0.40	0.42	0.33	→
0.61	0.47	0.38	0.41	0.28	→
0.62	0.44	0.35	0.41	0.28	→

Figure 2. Top view of flume area with distribution of u^* values at a flow of 22.9 liter/min in the direction of the arrows. The trip bar would thus be at the left end of the flume area.

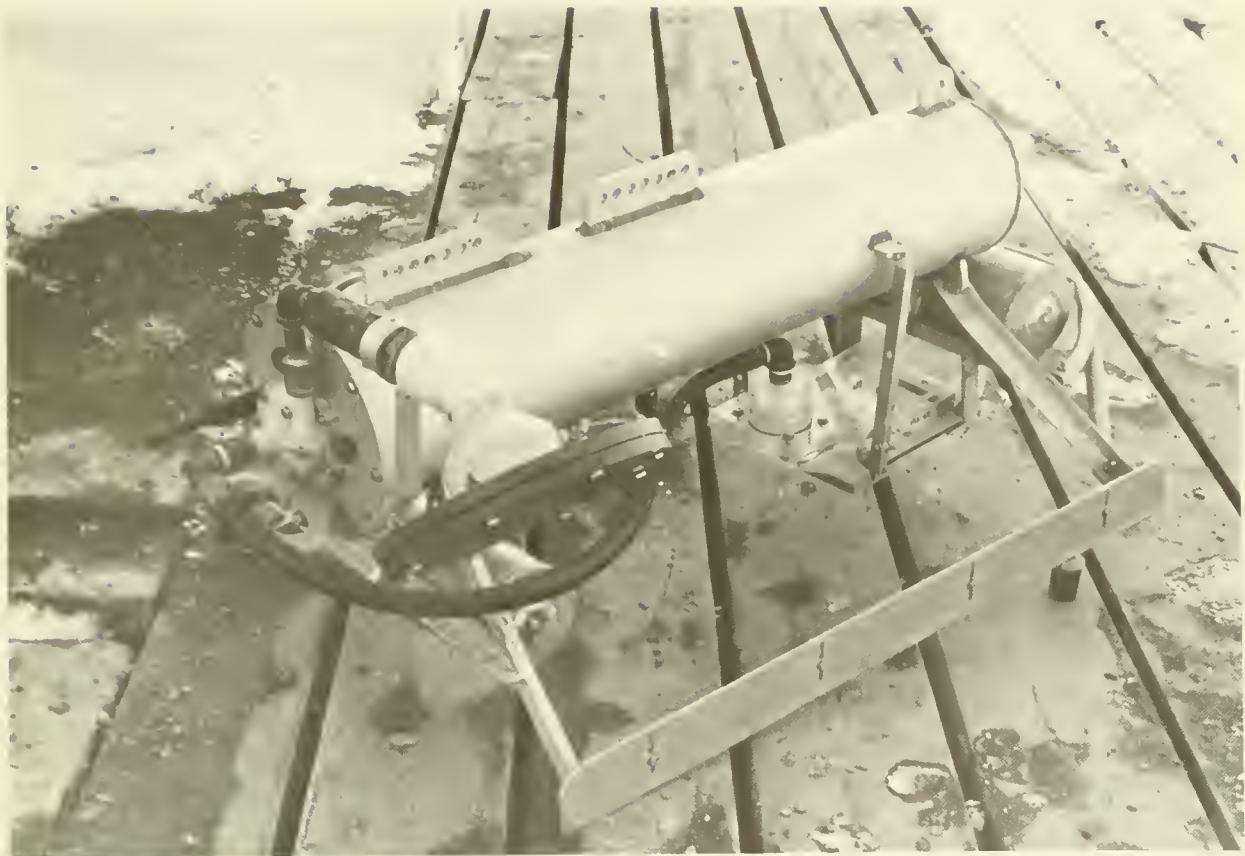


Figure 3.

Photograph of lander with which to deploy the FLS by either SCUBA diver or Delta submersible.

painted on the outside of the housing corresponding to the position of the reed switch inside. A time-delay relay was incorporated into the circuitry so that it was necessary to hold the magnet near the target for 5 seconds (adjustable between 1-30 seconds) before the pump started, to avoid accidental starts. A 3 1/2 " diameter Lexan porthole on the side of the housing allowed viewing of a control panel containing indicator lights showing initial switch actuation, time-delay, and pump operation, and an LED digital clock showing pump running time in seconds. A digital display turbine-type flow meter was also incorporated but was not used in these initial experiments.

The intake pump is connected by rubber hose to the sampling flume, with the outlet connected to the filter assembly by PVC pipe. The filter assembly was similar to the JSL unit but fabricated of welded PVC instead of aluminum. A bronze non-return valve between pump and filter prevents back flow of water and sluff from the filter after the pump is switched off.

The welded end of the housing contains a pressure relief valve set at 2 psi, to prevent excessive pressure build-up in the housing due to either leakage at depth or severe temperature differences and consequent danger upon opening the housing. There is also an O-ringed plug providing access to a vent in the battery housing, and a throughhull penetrator from the batteries to a connector for charging and/or monitoring of battery condition. The batteries have sufficient capacity to run the pump for approximately 10 min but recharging is performed routinely after each dive, a process requiring 10-15 min. During the charging the housing access plug is removed and the battery housing vent unscrewed to prevent build-up of hydrogen and potential explosion in combination with brush arcing from the DC motor.

The tubular housing is supported on two skids, 24" apart, running the length of the housing and adjustable vertically so that the weight on, and thus penetration of, the flume could be varied. The complete sampler unit weighs approximately 70 lb in air, but, with the addition of two small aluminum tubular buoyancy tanks, only 1-2 lb in saltwater, allowing it to be easily maneuvered and emplaced. A multihole mounting plate on top of the housing allows for variation of the suspension point from the sub in order to experiment with different emplacement attitudes. Operation depth limit for the complete device is 1,000 ft, with a designed failure depth of 3,000 ft.

Deployment of the FLS

There are a variety of problems associated with gently emplacing the FLS into a soft and easily resuspendable sediment, with a need for vertical positioning accuracy in areas of occasionally high turbidity. The solutions to these problems are different for the various dive systems used to date.

The deployment of the FLS with the Johnson Sea-Link involves attaching the flume to the wrist of the sub's robotic arm. The deployment necessarily occurs at a distance of 2-3 meters from the cockpit observers; this distance, combined with poor visibility conditions and the reducing lens effect of the Plexiglas sphere, has made it necessary to attach a small video camera to the wrist of the hydraulic arm. The cockpit observers can put the flume into a roughly horizontal position and bring it to within a few decimeters of the sediment-water interface before using the wrist camera. The flume must be emplaced very slowly, with the hydraulics of the arm turned down as far as possible, in order to avoid a bow wave effect from the descending flume. The small height of the flume when emplaced, coupled with the need to position the trip bar exactly on the sediment-water interface, require $+/- 1$ mm accuracy in positioning in order to obtain the u^* distribution measured in the laboratory. This fine positioning is at the limit of the capability of the sub, and often many tries are necessary before a good emplacement results. A common problem is a "dust cloud" set up by the sub during the landing process, which is solved by pointing the sub into whatever current is present and slowing inching the sub forward after landing. A second problem is hydraulic creep of the arm during the pumping process, which can lead to several mm of vertical movement of the flume during several minutes, which could occasionally be solved with fine-tuning of the hydraulics by the sub pilot.

After the flume is satisfactorily emplaced, the operator turns on the pump and monitors the flow meter inside the cockpit. Good stability of flow ($+/- 10 - 15\%$) for many minutes was obtained.

The Delta system deploys the lander-flume assembly by suspending it from a block on the bow plane; the assembly is lowered by the sub pilot with a manual pulley system under direction from the scientist/operator. Potential dust cloud problems are solved in the same manner as for the JSL, with a soft landing followed by inching into the current. The Delta system allows direct observation of the flume by the scientist/operator, due to a distance of no more than a meter and no reducing lens effect. The manual lowering allows for a very slow descent, and no bow wave problems are encountered. The weight of the lander interacts with the firmness of the sediment to control the depth to which the lander-flume assembly sinks into the sediments; it is necessary, therefore, to keep the negative buoyancy sufficiently low to avoid too great a penetration of the flume into the sediments. The final insertion into the sediments, then, is accomplished by the scientist, using the mechanical arm to push the assembly down. The magnet with which to trigger the motor is mounted at the end of the same arm, and the magnet is simply held next to the target on the aluminum housing for the desired time.

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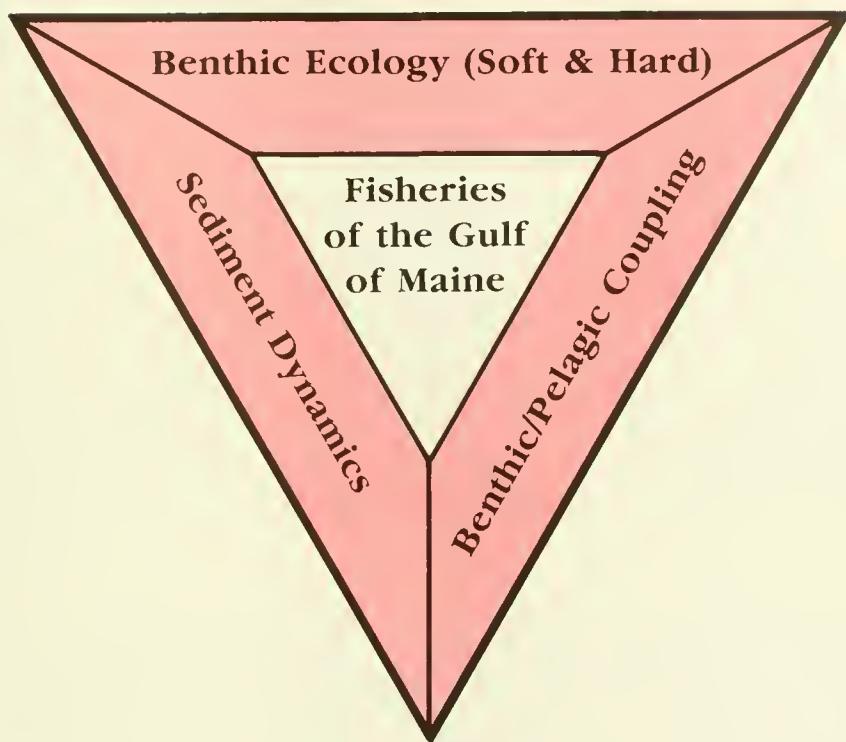
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Fisheries



SESSION SUMMARY: FISHERIES

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Fishing grounds and spawning sites in the Gulf are well-known and the question to be answered is why these geographic areas continue to produce commercially valuable living resources. Although survey work such as the National Marine Fisheries Service spring and autumn groundfish surveys and annual scallop survey has greatly improved our understanding of the distribution and abundance of these resources, the question of sustained yield continues to elude scientific investigators. An appreciation of the finer scale biological interactions that occur on these fishing grounds and at herring spawning sites may give us the necessary understanding to predict what is going to happen to a particular resource and why. Certainly it is known that the physical system defines the environmental range within which a species exists, but the current level of our knowledge of a species' environmental requirements is not adequate for biological resource management. Fisheries exist well within the bounds of the physical system that drives the Gulf of Maine so what is needed is research aimed at the biological events that produce and sustain the fisheries per se. Site-specific research in locations of known biological importance will eventually provide the data base for resource managers to extrapolate up to the scale necessary for resource management. Modern undersea technology as applied to fisheries research is the first step in this direction.

The use of manned submersibles and remotely operated vehicles (ROVs) for quantitative studies of fishery resources introduces a finer scale of resolution than previously possible. The three papers in the fisheries section of this symposium reflect the capabilities of modern undersea technology to conduct experiments and make such observations at depths well below SCUBA range. The paper by Stevenson and Knowles, for example, describes the detailed physical characteristics of four herring egg beds along the Maine coast. It does so with a precision only achievable with in situ observation. Similarly the successful recovery of tagged scallops described by Berkman could only have been done with direct observation of the experimental site. The paper by Langton and Robinson also reflects precise transect work obtainable with today's electronic navigation and surface to submersible communication.

The study of herring egg beds employed a variety of observational and sampling techniques to characterize spawning grounds in eastern Maine. (Herring aggregate and spawn

depositing eggs in adhesive mats on the sea floor that then develop and hatch in approximately ten days). The ROV Minirover was used together with surface deployed sampling gear to define the extent and density of egg deposition and the nature of the spawning substrate. The egg mat was fairly thick, measuring from 1 to 3 cm or from 20 to 30 eggs deep. This is generally thicker than previous reports for the Gulf of Maine, but was not a factor in egg mortality. The percentage of dead eggs in most subsamples was negligible. The successful hatching, despite the high egg density, presumably is a result of the strong water currents and consequent aeration of the egg bed. Substrate type was not clearly a controlling factor in defining egg beds. Distinct egg bed perimeters observed in some locations were defined by changes in substrate; in other locations where egg cover declined more gradually the substrate inside and outside the bed was similar. What was apparent was that gravel is a necessary component of the spawning substrate. The conditions along the eastern Maine coast are optimal for the successful spawning of herring and hatching of the eggs. Egg density reached a high of 7.2 million eggs m⁻² on the primary study site. The estimated weight of spawning herring required to produce the quantity of eggs observed was 8,000 to 15,000 metric tons, or 6 to 7% of the estimated spawning stock for the coastal Gulf of Maine stock.

The two papers on sea scallops are related in that the field work was done on the same scallop beds although the objectives of the studies were quite different. The paper by Berkman utilized manned submersibles to conduct tagging and caging experiments. At two locations in the Gulf, tagged scallops and scallop shells were placed both inside and outside cages. The following year the locations were revisited and the scallops recovered for examination of the epizooic shell community, deterioration of the tagged shells, as well as movement, growth and mortality of the live scallops. Unfortunately, both experimental sites were disturbed by trawling but a significant percentage of the scallops and shells were recovered from the Fippennies Ledge area. At this location 58% of the tagged live scallops were recovered in close proximity to the release site. In other words, these adult scallops moved little over the year. They did, however, grow and their growth rate was comparable to other published data on the growth of similar sized animals. What's of particular interest in the paper is the discussion of estimating natural mortality by use of "clapper" shells. Previous reports have used the time for deterioration of the shell ligament to estimate mortality. Berkman's study found that shell ligaments deteriorated quite slowly and suggests that shell valves may stay attached longer than previously thought; from as little as 20 weeks to over one year. Thus the "clapper" technique for assessing mortality needs to be re-evaluated. Another aspect of the paper was an assessment of the variation in the epizooic shell communities. There was a significant difference in the community that established itself on the inside and outside of scallop shells. Over the year, 55 species settled on the scallop shells and established assemblages with different degrees of

diversity and biomass although live and dead scallops offer a structurally similar substrate.

The paper by Langton and Robinson utilized quantitative photographic transects to characterize the macrobenthic invertebrate fauna on three scallop beds in the western Gulf of Maine. The scallop itself, occurred in patches rather than being randomly distributed over the sea floor. The distribution of scallops, even at their lowest density, was best described by a negative binomial equation. The relation between scallops and the other two dominant invertebrates was also investigated. On Fippennies Ledge the sabellid worm was found to significantly co-occur, or have a positive association, with the scallop while the burrowing anemone was negatively associated with scallop occurrence. At the other two study sites the species associations were not as clear, however, scallop density was much lower. It was suggested that the faunal associations broke down because of scallop dredging activity. The sabellid worm and burrowing anemone are both capable of retracting into the sediment while the scallops would be removed by the dredge.

SEA SCALLOP TAGGING EXPERIMENTS USING MANNED-SUBMERSIBLES

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ABSTRACT

Sea scallops were tagged and released on offshore ledges in the Gulf of Maine to study their growth, movement, mortality and shell deterioration. After one year, seventy percent of the tagged live and dead scallops were recaptured with manned submersibles. All of these scallops were found within a ten meter radius of their release site. Growth of these scallops was similar to estimates made from other studies, however their mortality was higher. The deterioration of their shells showed that the valves may be paired for periods substantially longer than one year. These data suggest that the application of "clappers", as a mortality estimator, should be reevaluated.

INTRODUCTION

Understanding the ecology of the sea scallop, Placopecten magellanicus, is important for both science and resource management. It is a conspicuous component of the coastal benthic community in the western North Atlantic as well as a much enjoyed seafood. Investigations have included laboratory studies (Merrill 1961), the use of benthic trawls (Dickie 1955, Caddy 1979, Posgay 1979), SCUBA studies (MacDonald and Thompson 1985 and 1986), and submersible observations (Caddy 1970). Submersibles were used in this study to manipulate sea scallop tagging experiments on offshore scallop beds in the Gulf of Maine.

Live and dead tagged scallops were released for a period of one year to evaluate shell deterioration and the validity of "clapper" mortality estimates (Dickie 1955). The biomass of the epizooic assemblages on the scallops also were investigated because they may be related to how long a sea scallop has been dead (Merrill et al. 1966). Scallop growth and mortality were measured to determine the effect of the tags, and tagged scallop movement was analyzed to assess whether results from tagging studies can be generalized to the local scallop population.

METHODS

The Sea Scallop Tagging Experiments

Scallop collection and preparation.

Sea scallops were collected with SCUBA in the vicinity of Boothbay Harbor, Maine, during the summers of 1985 and 1986. These scallops were brought back to the laboratory at the Maine Department of Marine Resources and held in running seawater aquaria. Each scallop was measured with vernier calipers along its height, length and width axes, and would be remeasured to determine its growth. The epizooic assemblages on the upper and lower valves were photographed and then removed.

Scallop treatments.

Live tagged scallops were used to evaluate growth, movement and mortality. In 1985 the live scallops were tagged with red plastic numbers embedded in epoxy on the shell (Hudson 1972), and in 1986 by inserting a green spaghetti tag through a hole drilled in the upper valve above the byssal notch (Posgay 1963). In addition, dead tagged scallops were used as a control for evaluating shell deterioration. These scallops were killed immediately before release, and were kept in running seawater aquaria so that the ligament and resilium of the shell hinge would not deteriorate faster than natural. These scallops were tagged by drilling a hole through both valves at the peripheral margin adjacent to the umbo and then attaching an eight-inch plastic cable-tie loose enough so that the shell could fall apart naturally.

The recaptured scallops were separated into five treatments based on the potentially different shell habitats which could be colonized by epizooic species. These were epizooic assemblages on the exterior shell surfaces of the live tagged scallops which lived (LIVETAG); on the exterior (LIVEDE); and interior (LIVEDI) shell surfaces of the initially live tagged scallops which died; and on the exterior (DEADE) and interior (DEADI) shell surfaces of the initially dead tagged scallops. Thirty live scallops from the local population (LIVE) also were collected.

Cages were constructed to protect the experimental scallops from being disrupted by commercial trawlers and to insure that some of the experimental replicates would be retrieved. Five-foot square cages were built from quarter-inch steel rods and one-inch square plastic-coated wire mesh. Each cage was constructed so that it could be opened and locked using a submersible manipulator. Ten live and 10 dead scallops were placed in each cage. Three cages were placed in each area so that a cage effect (Jamieson et al. 1982, Schmidt and Warner 1984) could be evaluated. Twenty-five live and 25 dead tagged scallops were released adjacent to each of the cages, except during 1986 when 65 live and 65 dead scallops were released

together in a boulder-protected area after one of the cages had been pulled off the site.

Tagged scallop release and recapture.

The scallops were transported to Jeffreys Ledge ($42^{\circ}52'$, $70^{\circ}08'$) onboard the R/V EDWIN LINK. The three cages were attached to each other with polypropylene cord and then dropped from the side of the vessel onto a flat sandy bottom. The scallops were then dumped in and around the cages from plastic buckets carried down by the submersible JOHNSON SEA-LINK I (Harbor Branch Oceanographic Institution) on 14 July 1985. The cage location was determined with LORAN C. In addition, a 37 khz pinger surrounded by steel rods and encased in a cement block was left next to the cages. This experimental site was revisited on 4 July 1986.

The scallops were transported to Fippennies Ledge ($42^{\circ}45'$ $69^{\circ}15'$) onboard the R/V ATLANTIC TWIN. The three cages were dropped overboard individually in a large boulder field. Scallops were looped by their spaghetti tags on a cord strung along the inside of each cage. This ripcord was pulled on the bottom by the manipulator arm of the submersible DELTA (MARFAB), allowing the scallops to settle inside the cage on 6 July 1986. The scallops on the outside of the cages were dumped from a cloth bag carried down by the submersible. The relative position of each of the cages was noted, and these sites were revisited on 26-28 June 1987.

RESULTS

Tagged scallop recapture

The 1985 release site on Jeffreys Ledge had been disturbed by extensive trawling in the area. Unfortunately, all that was recovered were an overturned pinger in a cement block, 23 dead tagged scallops (DEADE and DEADI), and one live tagged scallop (LIVETAG). Even after a thorough search of the vicinity, the three cages were not found. Trawl marks, occasional middens of shucked scallops, and piles of rocks were further evidence of the extensive trawling in the area.

Conversely, two of the three 1986 release sites on Fippennies Ledge were undisturbed. The one cage that had been moved by trawlers was found, but there were no scallops collected for that site. The scallops from the other two sites were collected individually with the manipulator arm on the DELTA and then placed in a cloth bag on the side of the submersible. These results are summarized in Table 1.

Table 1. Tagged scallop recapture Fippennies Ledge, Gulf of Maine July 1986 - July 1987

Scallop Treatment	Number Tagged	Number Recaptured	Percent Recapture
Initial Live	105		
LIVETAG		20	19
LIVEDE+LIVEDI		41	39
TOTAL		61	58
Initial Dead	105		
DEADE+DEADI		85	81
TOTAL		85	81
TOTAL 210	146	70	

This data includes two living and 18 dead caged scallops. Because a significant sample size of tagged scallops was collected outside of the cages and because of the potential experimental errors introduced by the cages, none of the caged scallops were used in the following analyses.

Tagged Scallop Population Characteristics

Growth.

The Walford regression calculated from the initial and final shell height measurements for the recaptured live tagged scallops (LIVETAG) was $L_{t+1} = 36.01 + 0.96L_t$ with an r-value of 0.97. The initial shell height and growth rate for these scallops is shown in Figure 1 (r = 0.82).

Movement.

Sixty percent of the initially live tagged scallops (LIVETAG, LIVEDE, and LIVEDI), from the two undisturbed release sites on Fippennies Ledge, were recaptured. This high percentage of scallops, recaptured within a ten meter radius of where they had been released a year earlier, demonstrates that tagged sea scallop movement was minimal. The live tagged scallops (LIVETAG) recessed into small pits, and were observed to be uniformly spaced.

Mortality and shell deterioration.

Sixty-seven percent of the uncaged tagged live scallops died during the yearlong experiment, and 80 percent died inside the cages. The tagged live scallops that died (LIVEDE and LIVEDI) were used to evaluate the condition of the hinge and resilium over different lengths of time. The length of time that a

scallop had been dead was estimated by dividing the total shell growth by the shell growth rate for that specific sized scallop as shown in Figure 1. The tagged live scallops (LIVEDE and LIVEDI) had been dead for $8.5 + 3.5$ months, whereas the tagged dead scallops (DEADE and DEADI) all had been dead since the beginning of the experiment. Seven percent of the initially live tagged scallops (LIVEDE and LIVEDI) had fractured hinges, suggesting predation. Figure 2 shows how the hinge and resilium deteriorate after the sea scallop dies.

Sea Scallop Epizooic Assemblages

Biomass and composition.

The relationship between epizooic settlement and the amount of time that a mollusc has been dead have been investigated in oysters (Gunter et al. 1957), clams (Driscoll and Swanson 1973), and scallops (Merrill et al. 1966). There were 55 species from 8 phyla represented in the offshore tagged scallop epizooic assemblages. These assemblages included juvenile sea scallops (less than 1 cm in height) and small Cancer borealis, both of which were found inside of the dead tagged scallops. Figure 3 shows that there were consistent differences between the epizooic biomass on the interior and exterior shell surfaces of the initially live tagged scallops (LIVEDE and LIVEDI) and of the dead tagged scallops (DEADE and DEADI). The differences between these treatments were compared with paired t-tests and were significant at $P = 0.05$. Jackknifed comparisons of species richness (Heltshe and Forrester 1983) also indicated that these assemblages were significantly different.

DISCUSSION

Tagging studies have been an important means of assessing the growth, movement and mortality of the sea scallop. However, interpretations from these studies have been based on low returns (less than 15 percent), experimental errors introduced by scallop dredges, and by inaccurate methods of reporting recapture information (Posgay 1963, Merrill et al. 1966). The use of manned-submersibles provided a method for recapturing over 58 percent of the tagged live scallops (LIVETAG, LIVEDE and LIVEDI) and an in situ view of the tagged scallop population.

Because a large percentage of the tagged scallops were recaptured, it is possible to speculate how the tags affected sea scallop mortality and growth. The annual mortality rate, estimated for the recaptured tagged scallops that died between July 1986 and July 1987, was over 65 percent. Mortality estimates based on the proportion of "clappers" (dead scallops with paired valves; Dickie 1955) in the population are around 0.10 (Merrill and Posgay 1964). However, the tagged scallop growth rates calculated in this study were not significantly different from those of other studies (Merrill et al. 1966). These data suggest that while the tagged scallops were alive they

TAGGED SEA SCALLOP SHELL GROWTH
FIPPENNIES LEDGE, GULF OF MAINE
JULY 1986 – JULY 1987

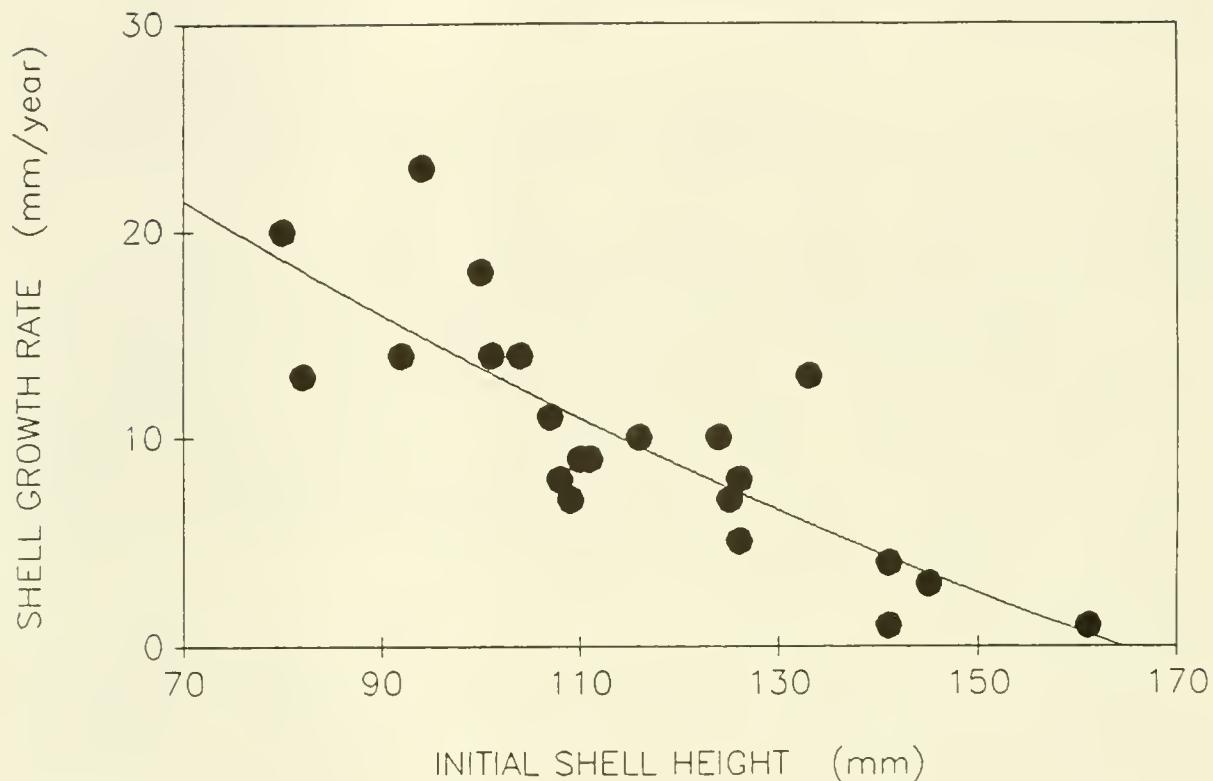


Figure 1. The shell height growth of the tagged sea scallops which were recaptured on Fippennies Ledge, in the Gulf of Maine, after one year.

TAGGED SCALLOP DETERIORATION
FIPPENIES LEDGE, GULF OF MAINE
JULY 1986 – JULY 1987

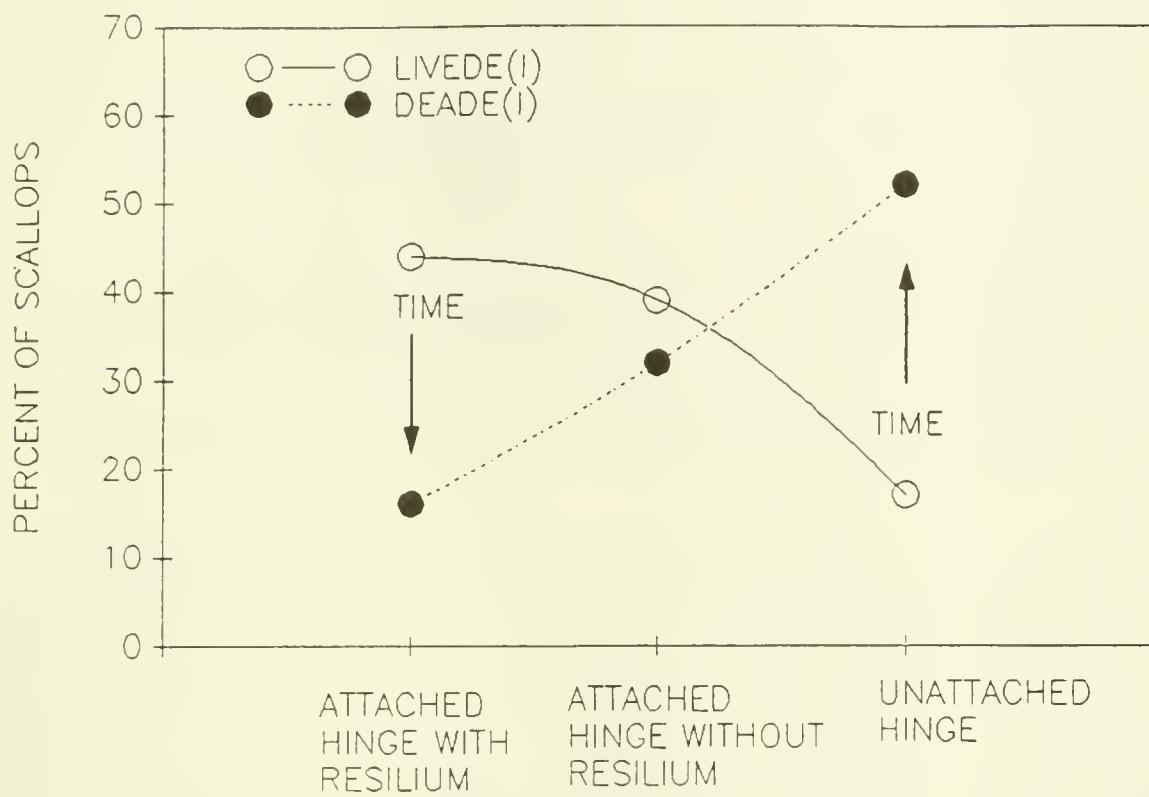


Figure 2. The tagged live scallops which died (LIVEDE and LIVEDI) had been dead for 8.5 ± 3.5 months, whereas the dead tagged scallops (DEADE and DEADI) had been dead for the entire year. With increasing time the percent of attached valves decreased and the percent of unattached valves increased. After one year, 50 percent of the dead scallops had unattached valves.

SEA SCALLOP EPIZOOIC BIOMASS COMPARISON
FIPPENNIES LEDGE, GULF OF MAINE
JULY 1987

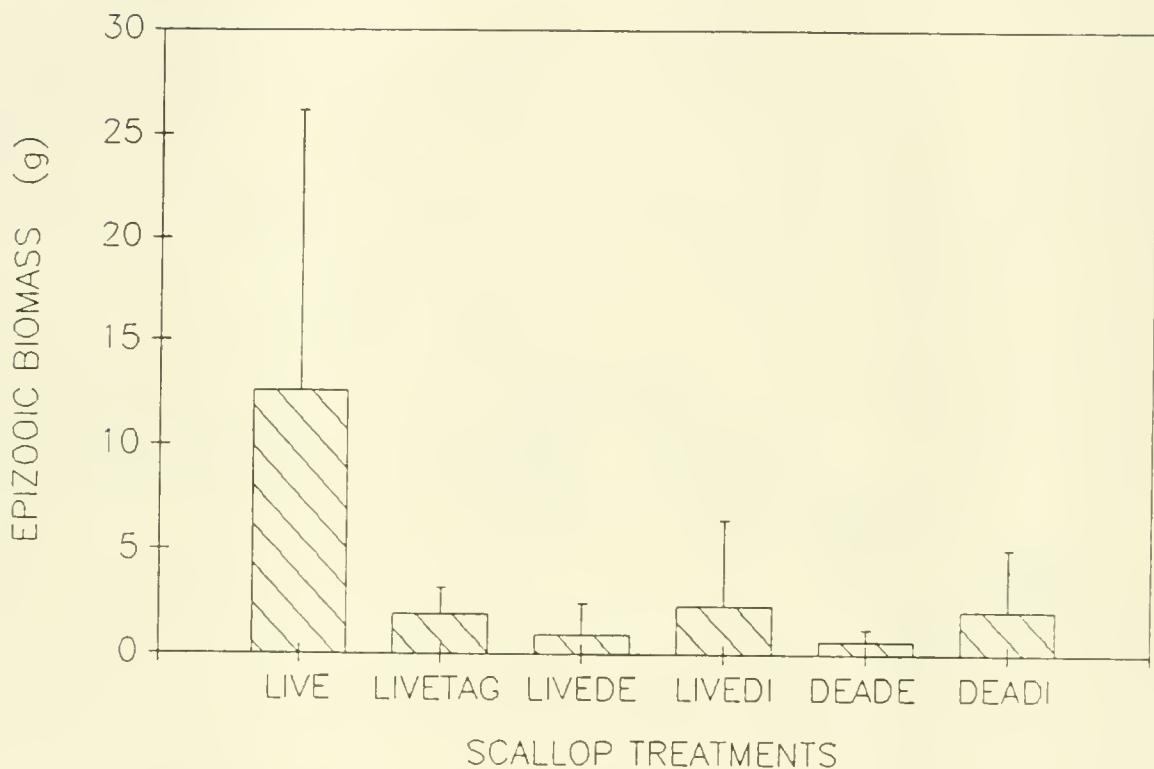


Figure 3. Epizooic biomass on the five scallop treatments. The biomass on the interior was greater and more variable than on the exterior of the dead scallop shells.

grew at a natural rate, but that their mortality rates may have been increased by the tags.

The "clapper" method of estimating mortality is dependent on the time that it takes for the valves to separate after the scallop has died. Based on laboratory experiments, Dickie (1955) suggested that it took an average of 14 weeks for the valves of the sea scallop to separate. Using shell deterioration in a natural population, Merrill and Posgay (1964) estimated that it took an average of 33 weeks for the valves to separate. The dead tagged scallop treatments (DEADE and DEADI) in this study show that after one year only half of the scallops had separated valves (Figure 2). The tagged live scallops that died (LIVEDE and LIVEDI) show that only 17 percent of the scallop's valves had separated after 8.5 ± 3.5 months. Together, these scallop treatments demonstrate how the valves of the sea scallop deteriorate over time, from attached valves with a resilium to unattached valves without a resilium (Figure 3). These estimates, of how long the valves stay paired, vary widely and indicate that this aspect of the clapper mortality estimate should be investigated further.

The biomass of the epizooic assemblage on the interior valve of the sea scallop also has been related to the length of time that a sea scallop has been dead (Merrill and Posgay 1964). The biomass of the epizooic assemblages on the interior shell surfaces (LIVEDI and DEADI) was significantly greater and more variable than those on the exterior shell surfaces (LIVEDE and DEADE); see Figure 3. Yet, there was no trend between the biomass of the epizooic species on the interior valve surfaces and the period that a tagged scallop had been dead. The absence of this trend might be expected because epizooic species in the Gulf of Maine have seasonal settlement cycles (DePalma 1969), and they may not begin to develop until long after the scallop has died. The fact that epizooic species richness was significantly different between these assemblages suggests, however, that epizooic composition may be useful for assessing the length of time that a sea scallop has been dead.

These data clearly demonstrate that the adult sea scallops do not migrate because all of the recaptured individuals were found within a 10 meter radius of their release site. The live scallops were found in depressions in the sediment and the dead scallops were found on the sediment surface (Figure 4). As suggested from this study, tagged scallops do not distribute themselves randomly over large areas and therefore, caution must be used when extrapolating information from tagging studies to the natural population.

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POSSIBLE FLOW PATTERNS OVER SCALLOPS

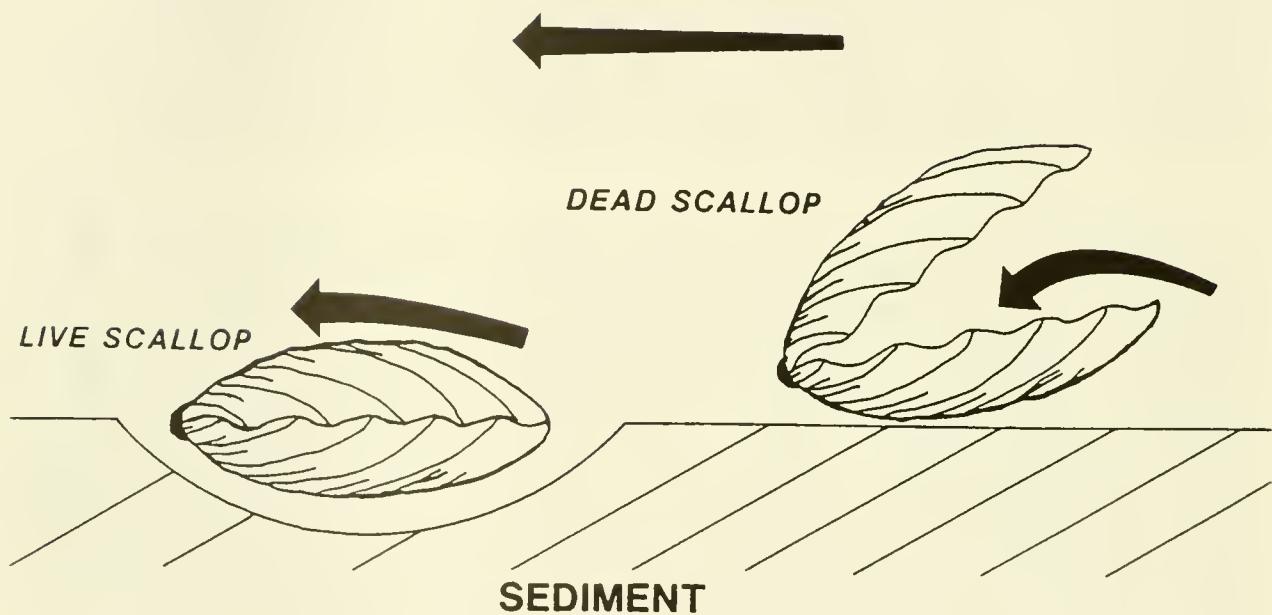


Figure 4. Position of live and dead sea scallop on the sea floor, and the possible current flow patterns over their shells.

Department of Marine Resources, dive team, and the invaluable ingenuity of the Johnson Sea Link and Delta crews are deeply appreciated. This research was supported by the National Undersea Research Program office at Avery Point, Connecticut, and by a National Science Foundation graduate fellowship.

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ECOLOGY OF THE SEA SCALLOP PLACOPECTEN MAGELLANICUS
(GMELIN, 1791) IN THE GULF OF MAINE, U.S.A.
- A PRELIMINARY REPORT

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ABSTRACT

In 1984 a study of offshore scallop beds was initiated in the Gulf of Maine using manned submersibles. To date, three scallop populations have been surveyed and quantitatively documented photographically. These populations occur on Jeffreys ledge, Fippennies Ledge and Platts Bank. The three study areas are physically and ecologically similar in many respects. At all sites the depth ranges from 198 to 290 ft. and sediment types range from sand to silty sand to cobbles and boulders. The dominant macrobenthic invertebrate fauna is similar with the sabellid worm, Myxicola infundibulum being numerically dominant. The two other important invertebrates are the burrowing anemones, Cerianthus sp., and the sea scallop, Placopecten magellanicus. Scallop density itself varies from a high of 0.98 ± 2.19 scallops per m on Fippennies Ledge to a low of 0.21 ± 0.50 scallops per m on Jeffreys Ledge with Fippennies Ledge being intermediate at 0.31 ± 0.80 per m. The actual number of scallops per 35 mm photo frame is extremely variable ranging from a density of 0 to as high as $19 \text{ scallops m}^{-2}$. The distribution of these data is best described by a negative binomial equation. Our statistical analysis has shown that the scallops are not randomly distributed over the bed but, rather, occur in clusters or patches even at the lowest densities observed on Jeffreys ledge. An analysis of the association between the scallop and the two other dominant macrobenthic invertebrates has shown a significant ($\chi^2 = 41.33$, $P < 0.05$, 1 d.f.) positive association between Placopecten and Myxicola and a significant ($\chi^2 = 7.66$, $P < 0.05$, 1 d.f.) negative association between Placopecten and Cerianthus on Fippennies Ledge. On Jeffreys Ledge and Platts Bank the data does not support the results described above for Fippennies, however, scallop density is much lower and it is suggested that this results in a breakdown of these faunal associations. On Jeffreys Ledge, for example, scallop dredge tracks were quite evident and it was observed that both Myxicola and Cerianthus occurred in

recently dredged areas suggesting that they simply retract into their burrows to avoid the dredge. As a consequence, removal of the scallops can occur without a negative impact on the two other dominant invertebrates.

INTRODUCTION

In a report on the sea scallop, Placopecten magellanicus, the New England Fisheries Management Council (1981) proclaimed that the entire Northwest Atlantic continental shelf of less than 100 meters depth might be suitable scallop habitat. While this statement may or may not be true, it emphasizes the point that very little is actually known about the ecology of this species. For an animal that is heavily fished, indeed possibly overfished, (Anderson, 1984), this lack of information compounds the problems facing resource managers. Knowledge of basic scallop biology is critical for predicting the resilience of the stocks to high fishing pressure. For the Gulf of Maine, this is particularly true because the catches since 1980 have been the highest on record (Anderson 1984). The following account is a comparative study of three offshore scallop grounds in the Gulf of Maine.

METHODS

This work was initiated in the summer of 1984 as a 3 to 5 year study of various offshore scallop grounds in the Gulf of Maine (Figure 1). Three different manned submersibles have been utilized to conduct quantitative photographic transects and make videotape recordings and general observations on three offshore banks. In this preliminary report, data from six out of a total of eight dives is described. One dive was made in 1984 on Platts Bank (Figure 2) using the submersible Mermaid II. In 1986 five dives were made using the submersible Delta. Two dives were on Jeffreys Ledge and three on Fippennies Ledge (Figure 2). In 1985 two dives were also made on Jeffreys Ledge using the Johnson Sea Link I but this information is not included here. In 1987 the Fippennies Ledge study site was revisited using the Delta submersible system and a total of six transects were completed. Analysis of these most recent dives is, however, not yet complete and the data is not included in this report.

Although each submersible system is unique, the transect technique was similar throughout the study. Generally, the submersible was launched at a preselected dive site and once on the bottom its exact location determined by ship to sub sonar and Loran C. Throughout the dive the sub and support ship were in frequent communication and location fixes were taken at regular (10 to 15 minute) intervals, whenever the diver noted a unique bottom feature, or when the submersible changed direction. When the submersible was stationary, during a location fix, the video camera was used to document bottom features; also, when the submersible was traversing slowly over the bottom video pictures were often taken. Random still color photographs, 35 mm, were taken at 10 to 15 second intervals over the entire transect.

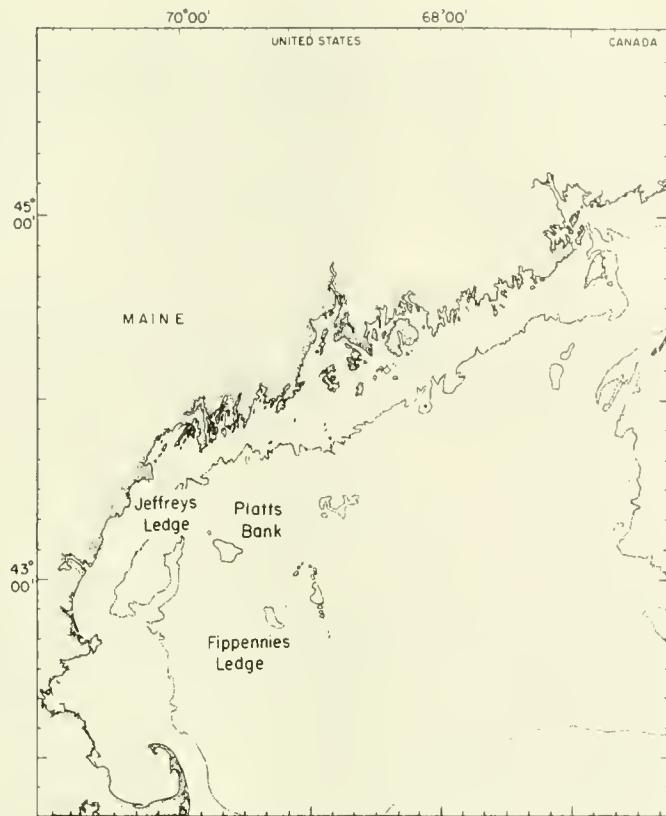


Figure 1. Map of the western Gulf of Maine, USA, showing the three study sites.

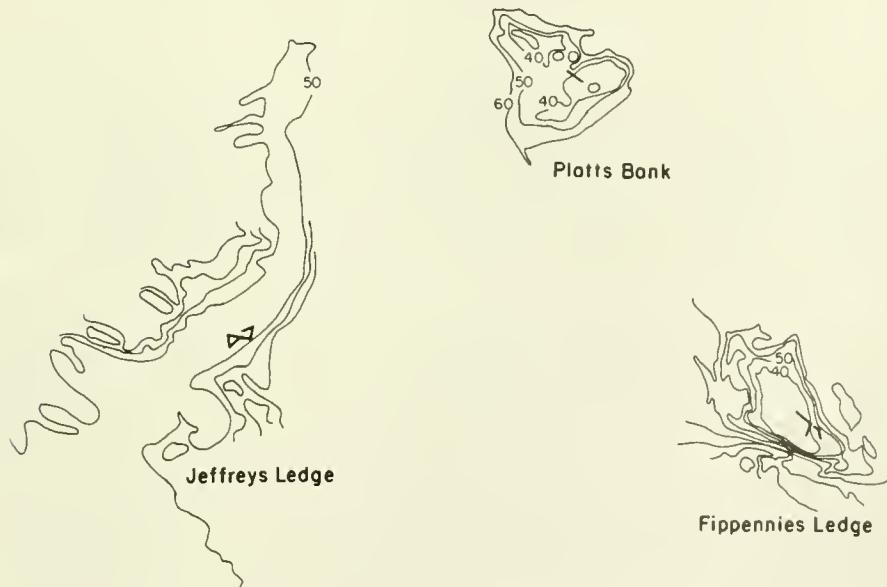


Figure 2. Depth contours of three study sites with submersible dive tracks indicated by the heavier lines. Depths are in fathoms.

There were approximately 150 to 250 photographs per dive. Total dive times varied from 1.5 to 2.75 hours but were usually at least two hours in duration. The amount of sea floor covered varied on each dive, depending on current speed and direction, but generally approximated one nautical mile. Throughout the dive the diver scientists recorded observations on the fauna, bottom/sediment type and other information on a portable cassette recorder.

In the laboratory, four data sets for each dive were available for analysis. 1) videotapes, which include pictures and audio; 2) 35 mm photographs; 3) a transcript of the diver scientists observations and 4) the ships bridge log. For quantitative analysis the 35 mm color photographs were the most valuable, although interpretation of these data were greatly enhanced by reference to both videotapes and the scientists' observations.

Each frame of the 35 mm color photograph was examined using a light table and 5x lens. Data frame information was recorded (i.e., frame number, date and time) and observations were made on the sediment type. Animals were identified to the lowest possible taxa and the number of individuals in each taxon were recorded. In the case of colonial forms, the number of individuals per frame was meaningless or could not be counted so they were simply noted as "present." The total individual frame area evaluated using the Delta was 1.24 m^2 and using the Mermaid II it was 0.66 m^2 .

RESULTS

Study Sites

The three study areas are physically similar in many respects. They all occur in the western Gulf of Maine (Figure 1) and have all been considered excellent fishing grounds in the past (Rich, 1929). Based on our observations, the areas are still being fished today with Jeffreys Ledge being dragged most heavily. (An experimental site we established in 1985 on Jeffreys Ledge had been destroyed by dragging when we returned to the location in 1986). The depth of the study sites on the three banks is similar, ranging from 198 to 290 ft. Similar sediment types were found on each of the three banks. Over the course of a single dive, however, sediments were observed to range from a sand to silty sand to cobbles and boulders. In the areas of highest scallop density (Fippennies Ledge) the sediments were, usually sandy and occasionally included some shell hash and small rocks. In some instances, the surface of the sediments appeared to be more of a silty/organic sand where there were tubes formed by amphipods or small polychaete worms.

Faunal Characteristics

The fauna in the three areas is quite similar with a total

of 26 taxa being identified in the photographs to date. In all three areas the dominant invertebrates are the sabellid worm, Myxicola infundibulum, burrowing anemones, Cerianthus sp. (most likely C. borealis), and the sea scallop, Placopecten magellanicus.

Scallop Density and Distribution

Scallops occur in varying densities at the three sites. They are most numerous on Fippennies Ledge where the mean density is 0.98 ± 2.19 scallops m^{-2} . On Platts Bank the density drops to 0.31 ± 0.80 m^{-2} while on Jeffreys Ledge it is even lower at 0.21 ± 0.50 m^{-2} .

The actual density of scallops per photo frame ($1.24 m^2$) on Fippennies Ledge (Figure 3) graphically demonstrates the extreme variability in scallop densities over the course of three transects. Chi-square analysis of this photographic data was employed to compare the actual distribution of the population with that of a calculated Poisson distribution. In all cases the scallop distributions deviated significantly from the Poisson, indicating that the scallop distribution was not random. A negative binomial distribution could be fit to each of the data sets and adequately described the populations at the three sites, (Figure 4). These statistical techniques show that scallops are not distributed randomly over the grounds, even at the lowest density observed. In contrast to a random distribution, the contagious distribution of the variants in our analysis indicates that the scallops are located in clusters or patches over the bottom. To further illustrate this, the data for Fippennies Ledge and Jeffreys Ledge have been standardized to 500 photographs and the expected distribution of the number of animals per frame calculated from the negative binomial and plotted in Figure 5. In both cases the data follows a similar pattern with a rapid decline in the numbers of pictures containing multiple scallops. On Fippennies Ledge where the scallop density is the highest, the distribution tails off much more gradually.

Since the scallops show a clustered distribution the question arises as to the effect of quadrat size on the analysis. To evaluate this effect each photo from the highest density area on Fippennies ledge was subdivided into approximately 1/4, 1/2 and full frame (0.33 , 0.66 , $1.24 m^2$) and the number of scallops counted per quadrat. Morisita's index of dispersion (Elliot, 1983) was then calculated for each of the data sets and the data plotted in Figure 6. As quadrat size is decreased, Morisita's index of dispersion should approach a value of 1. Such a value indicates a random distribution, or in this case, a breakdown of the contagious distribution actually observed in the $0.66 m^2$ and $1.24 m^2$ quadrats. From this plot it can be inferred that scallops are generally separated by a distance of at least 25 to 60cm. Observations from the submersible confirm that although scallops are often clustered they do space themselves over the bottom. Rarely were scallops observed close enough to actually

be touching each other although no measures of interanimal distance were made.

Faunal Associations

The relationship between the three dominant invertebrates was evaluated with the emphasis on the specific relationship with the scallop. Figure 3 shows the number of scallops, myxicolid worms and cerianthid anemones per photo frame for the three dives on Fippennies Ledge. The general impression of the scientist divers was that myxicolids and scallops occurred together while cerianthid abundance was inversely related to scallop density. The photographic record confirms this qualitative observation. It is especially clear for DELTA dive 440 where the highest abundance of scallops was observed (Figure 3). To quantify these relationships, the species association between Placopecten and Myxicola, and Placopecten and Cerianthus was analyzed using 2x2 contingency tables (Southward, 1968). The occurrence, co-occurrence or absence of each species was noted for each photograph, disregarding the actual number of individuals of each species per frame, and the resulting data was analyzed for departure from randomness. The data for both Myxicola and Cerianthus were non-random, showing a positive association between Myxicola and Placopecten ($\chi^2 = 41.33$, $P < 0.05$, 1 d.f.) and a negative association between Cerianthus and Placopecten ($\chi^2 = 7.66$, $P < 0.05$ 1 d.f.). On Jeffreys Ledge and Platts Bank, where scallop densities are much lower, the data does not support the results reported above for Fippennies Ledge. On Platts Bank no significant relationships were found between Placopecten and either Myxicola ($\chi^2 = 0.03$) or Cerianthus ($\chi^2 = 0.0004$). On Jeffreys Ledge there was no significant relationship between Placopecten and Cerianthus ($\chi^2 = 1.19$) but there was a negative association between Myxicola and Placopecten ($\chi^2 = 12.03$, $P < 0.05$, 1 d.f.). This significant negative association is primarily the result of the occurrence of Myxicola in the absence of Placopecten. In an area heavily dragged for scallops, such as Jeffreys Ledge, a negative association might be expected.

Dredging Effects

During the course of the dive on Jeffreys Ledge, areas that were dredged were readily distinguishable from undredged, or at least not recently dredged, bottom. The most obvious feature was a change in substrate from the more organic/silty sand to a sandy gravelly appearance. Occasionally, piles of rock and scallop shells were observed, having obviously been emptied out of a dredge once it was brought to the surface. No concurrent dredging and diving took place so it is impossible to say how quickly the bottom recovers from dredging activity in this area. (Such a study is now under way by Dr. Fred Serchuk, National Marine Fisheries Service, Woods Hole, MA USA; see also Caddy, 1973). On the macrofaunal level, obviously scallops are removed by dredging but it appears that both Myxicola and Cerianthus are capable of retracting into the sediment below the cutter bar. The

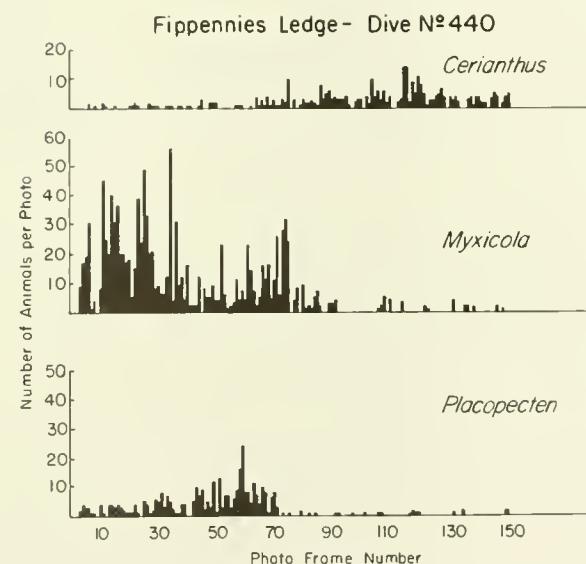
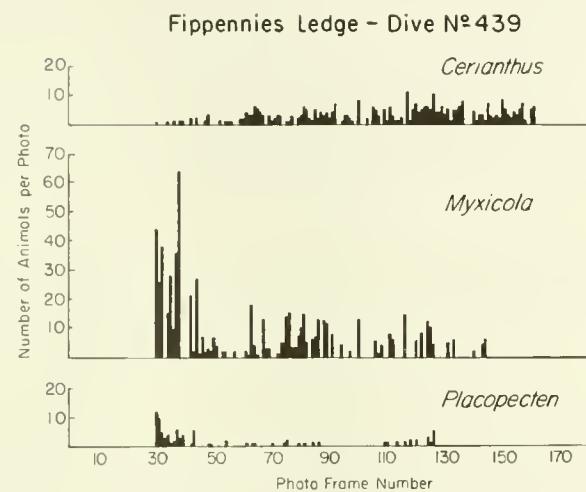
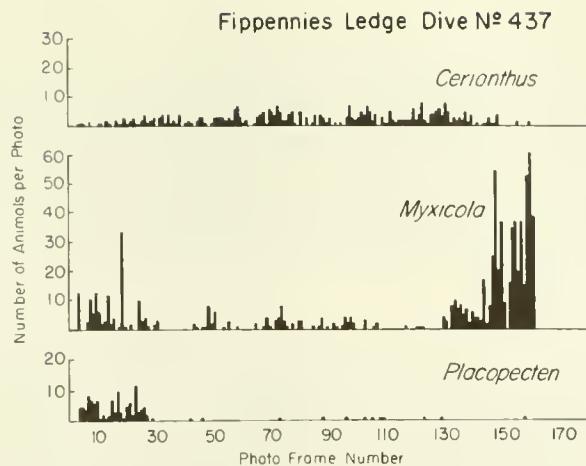


Figure 3. Numbers of the scallop, *Placopecten magellanicus*, the sabellid worm, *Myxicola infundibulum* and burrowing anemones, *Cerianthus* sp. per photo frame on the three dives on Fippennies Ledge. Photo frame area is 1.24m².

extent of dredging induced mortality on these sessile invertebrates could not be determined from our work although such mortality may be negligible while the fishing mortality on scallops can be substantial. The impact of dredging on the smaller invertebrates could not be assessed in this study but it may be significant if the change in substrate we observed in a dredged area persists.

DISCUSSION

There are a number of estimates of sea scallop densities available in the scientific literature (e.g., Table 1).

Table 1. Mean density estimates for Placopecten magellanicus from this study and scientific literature.

<u>Location</u>	<u>Density per m²</u>	<u>Authority</u>
Fippennies Ledge	0.98	This Study
Fippennies Ledge	0.92	Serchuk & Wigley (1984)
Jeffreys Ledge	0.21	This Study
Jeffreys Ledge	0.19	Serchuk & Wigley (1984)
Platts Bank	0.31	This Study
Digby, Nova Scotia	3 to 7	Dickie (1955); Bourne (1964)
N. Georges Bank	0.98	Caddy (1971)
Georges Bank	1.7 to 123 (spat)	Larsen & Lee (1978)
Gulf of St. Lawrence	0.1 to 4.8	Caddy (1970)
East Newfoundland	0.19 to 0.86	MacDonald & Thompson (1986)
West Newfoundland	2.3 to 4.0	Naidu (1969)

Throughout its geographic range scallop density on the various grounds generally ranges from a mean of 0.1 to <10 animals per square meter. The only exception to this is for spat densities on Georges Bank where a maximum density of 123 m⁻² was reported (Larsen and Lee, 1978). One interesting aspect of the reported mean densities from this study is the close agreement with the estimates calculated from the work of Serchuk and Wigley (1984). They report data from a scallop research vessel survey conducted in 1984, using a commercial dredge, throughout the U.S. northwest Atlantic. The Gulf of Maine sampling was concentrated on Jeffreys and Fippennies Ledges; our submersible study centered on their highest scallop density stations. Although the two studies were temporally separated by several years the dredge accounted for greater than 90% of the scallop population observed with a submersible. Such a comparison has to be viewed with reservation not only because of the time difference but also because scallop

density does vary substantially in both these regions and the submersible obviously did not cover the exact dredge path. Nevertheless, the level of agreement, even if somewhat serendipitous, is worthy of comment. In contrast to this high level of agreement between dredge and submersible comparisons, Caddy (1968, 1971) reported much lower scallop drag efficiencies ranging from 0.69 to 42.4% in a much more rigorous comparative submersible/ dredge study.

On the Richibucto grounds, Gulf of St. Lawrence, Caddy (1970) found that the scallop densities varied over the course of a dive track similar to the results reported here (see Figure 3). Caddy (op. cit.) tested the population distribution for departures from randomness and found the distribution to be contagious. On the scallop beds we studied the results are similar; scallops show a clustered distribution even at the lowest density observed. Our data was further analyzed to test for a model that adequately described the population structure. For both high and low density areas (i.e., Fippennies Ledge and Jeffreys ledge) a negative binomial model gave the best fit to the data (Figures 4 and 5).

Faunal associations at the three study sites in the western Gulf of Maine are very similar with three invertebrates being clearly recognized as dominant. The association between these three animals (the sea scallop, myxicolid worms and cerianthid anemones) is significant on Fippennies Ledge but is not as clearly defined at the other two sites. Ecologically the significance of these associations is not yet understood. The scallop and myxicolids are both suspension feeders, preying on similar sized particles (Dales, 1957; MacDonald and Thompson, 1985) while the cerianthids are carnivorous passive suspension or impingement feeders (Shepard et al., 1986). All three animals would require adequate currents and suspended material for feeding. Food availability may therefore be an important factor in the co-occurrence of these populations. Sediment type may also be important but detailed grain size analysis, organic content determinations, etc., are only now being done for the 1987 samples. As far as scallop occurrence is concerned observational data on sediment type has shown that scallops are most abundant on the more sandy substrates. Caddy (1970) also observed the highest density of scallops on sand rather than mud substrates.

Caddy and Carter (1984) evaluated faunal adjacencies on scallop grounds in the lower Bay of Fundy. Comparison of their faunal list from the eastern Gulf and ours from the western Gulf show a high degree of species overlap but a lower level of diversity (55 species in the east vs 26 in the west). However, further data collection and analysis, through 1987, may expand our species list. What is most interesting is that different species, apart from scallops, are dominant in the two regions. For example, Myxicola, our numerical dominant, does not occur in Caddy and Carter's faunal list although Myxicola's range includes

Distribution Models for Highest Density of Scallops on Fippennies Ledge

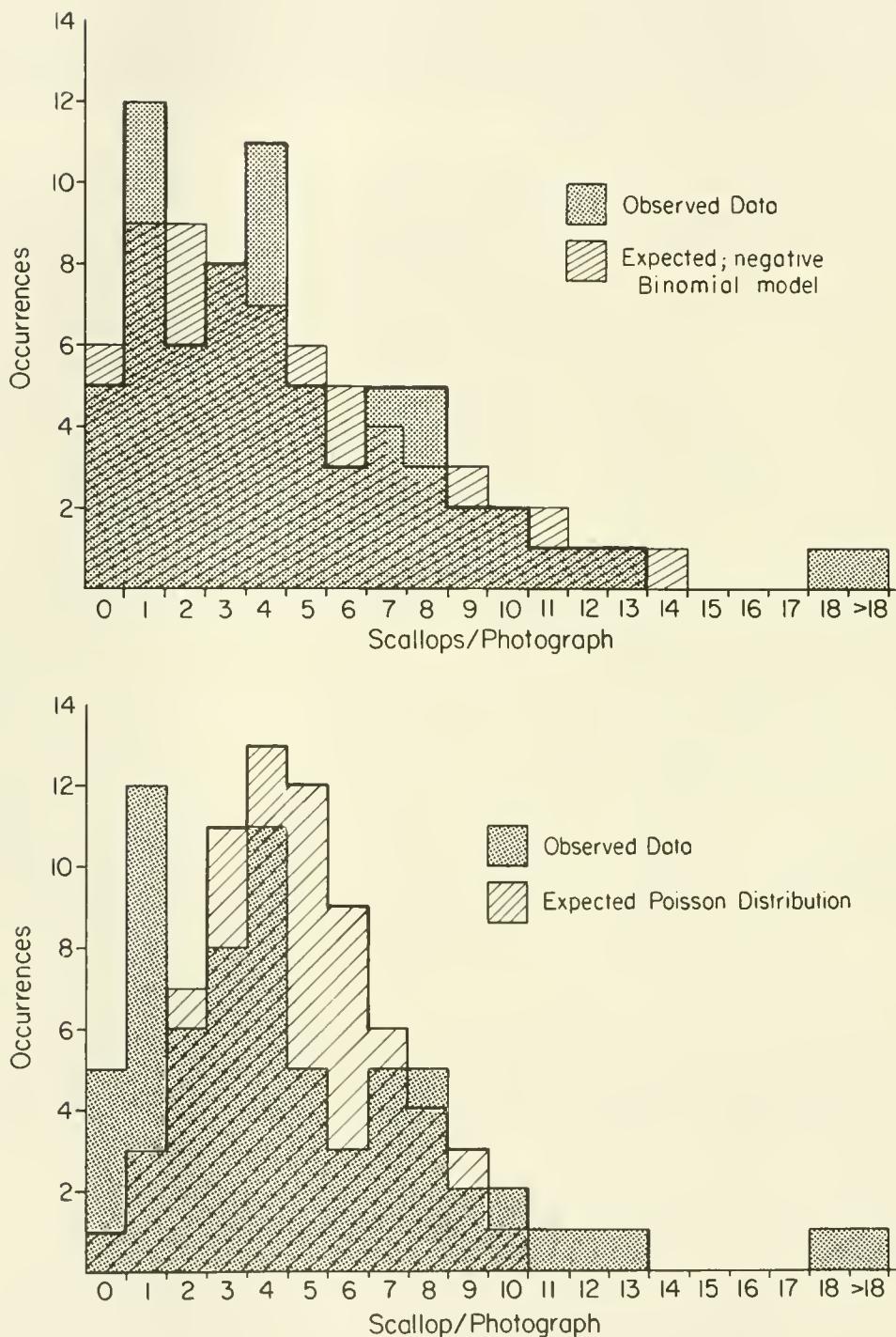


Figure 4. Distribution models for the highest density of scallops on Fippennies Ledge. 1) observed data with negative binomial model superimposed; b) observed data with Poisson distribution superimposed. The negative binomial model best fits the observed scallop distribution.

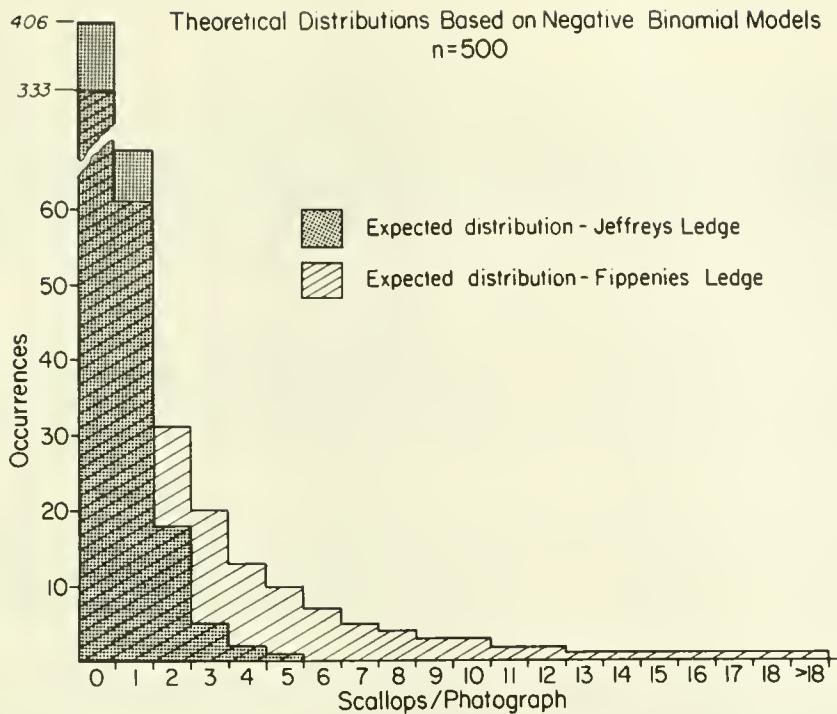


Figure 5. Illustration of the negative binomial model for number of scallops per photograph on Jeffreys ledge and Fippennies Ledge. Actual population density is much higher on Fippennies than on Jeffreys ledges as indicated by the much less truncated distribution in the above illustration.

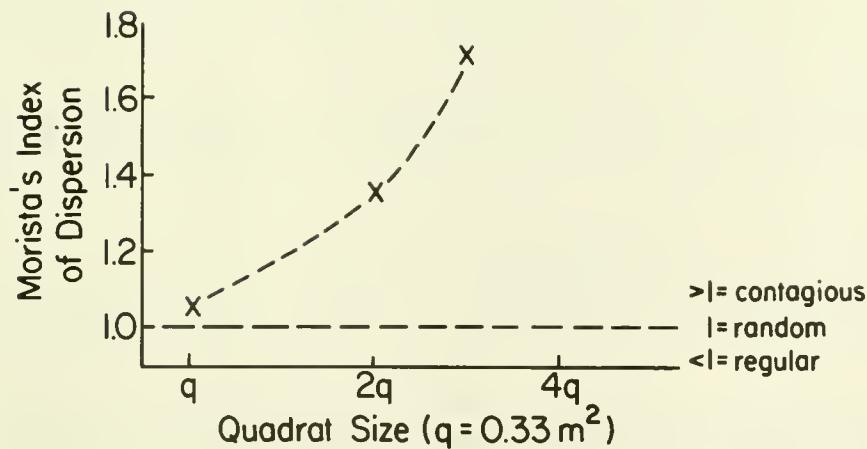


Figure 6. Plot of Morisita's index of dispersion for three different size photographic quadrats from the highest scallop density region on Fippennies Ledge. A value >1 indicates a contagious distribution while a value $= 1$ indicates a random distribution. The smallest quadrat size examined (0.33m^2) was statistically indistinguishable from a random distribution.

the Bay of Fundy. Pagurus which is important at the Bay of Fundy site has rarely been observed in our study in the western Gulf. Only sea anemones are dominants in both areas but Caddy and Carter (1984) do not identify the genera occurring at their study site in the Bay of Fundy.

ACKNOWLEDGEMENTS

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PHYSICAL CHARACTERISTICS OF HERRING EGG BEDS ON THE EASTERN MAINE COAST

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ABSTRACT

Herring egg bed surveys were conducted at four sites on the eastern Maine coast in 1985, 1986, and 1987 using a small remotely operated underwater vehicle (Mini-Rover), two types of benthic grab sampler, SCUBA divers, a depth recorder, and a side-scan sonar. Eggs were often visible in a continuous carpet 1-3 cm thick on a gravel, sand, and shell fragment substrate. Egg bed perimeters in some cases were fairly abrupt and were defined by changes in substrate. Eggs at one large site in 1986 were distributed over an area 0.8 km² in size in depths of 20-35 m. Egg cover at this site was absent or very light in rocky areas and where gravel was absent from surficial sediments. Egg density and abundance were higher in the deeper, offshore portion of this bed, reaching maximum values of 454/cc and 7.2 million/m². The total number of eggs spawned at this site was estimated as $2-3 \cdot 10^{12}$, requiring 8,000-15,000 metric tons of spawning fish. Egg mortality and differences in egg development rates at the top and bottom of the egg mat were negligible, indicating that the eastern Maine coast provides optimum conditions for herring egg deposition and survival. Sampling tools tested in 1987 are expected to expand the ROV's research capability by integrating video observations with quantitative samples of eggs, sediment, and larvae.

INTRODUCTION

Atlantic herring (Clupea harengus L.) deposit eggs in discrete beds on the bottom in depths ranging from very shallow water to approximately 100 m. Spawning occurs either in the spring or the fall; fall spawners spawn in deeper water than spring spawners. In the Gulf of Maine, herring spawn in the late summer and fall (August-November) in depths of 10-100 m. Principal spawning grounds are located in coastal waters southwest of Nova Scotia, in the vicinity of Jeffreys Ledge, and at various places along the Maine coast (Fig. 1). Herring spawned in large numbers on Georges Bank until the late 1970s. Herring eggs incubate for about 10 days before releasing small (5-7 mm) yolk-sac larvae into the water column.

Herring egg beds have been observed and studied in a variety of locations in the North Atlantic, mostly in shallow water environments which are accessible to SCUBA divers. Egg bed surveys have been carried out in deeper water (>30 m) primarily

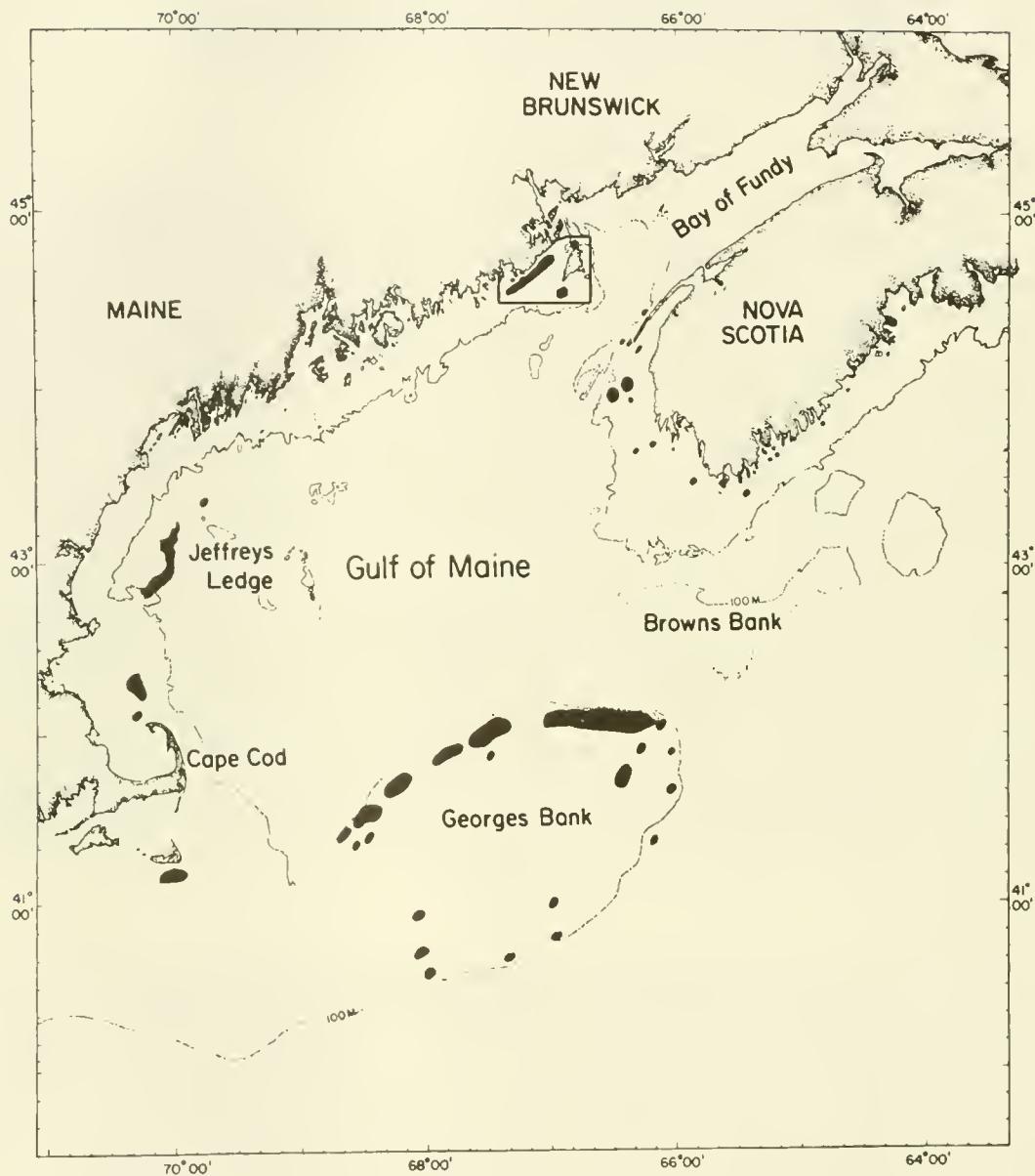


Figure 1: Herring spawning grounds in the Gulf of Maine. The box shows the location of the eastern Maine - Grand Manan spawning ground.

with the aid of benthic grabs and dredges operated from surface ships (Runnstrom, 1941; Fridriksson and Timmermann, 1951; Bowers, 1969; Pankratov and Sigajev, 1973). Other techniques have been used to locate spawning sites, including: (1) the capture of fully ripe adult herring; (2) the capture of other species which are feeding on herring eggs; and, (3) the collection of recently hatched larvae in towed plankton nets. None of these techniques, however, permit in situ observation and study of the egg beds or the egg bed habitat.

Deep water in situ work in the Gulf of Maine was carried out on egg beds on Georges Bank in 1970 with a submersible (Caddy and Iles, 1973) and on Jeffreys Ledge during 1972-1978 by personnel of the Northeast Fisheries Center's Manned Undersea Research and Technology Program using a variety of underwater techniques including submersibles, SCUBA divers, remotely controlled camera sleds, and an underwater habitat (Boyar et al., 1973; Cooper et al., 1975; McCarthy et al., 1979).

Egg bed studies were initiated by the Maine Department of Marine Resources (DMR) in eastern Maine coastal waters in the fall of 1983. Support during 1983 and 1984 was also provided by the University of Maine Sea Grant Program. Research activities during the first two years focused primarily on studies of larval distributions and physical and biological oceanographic factors affecting larval survival and westward transport along the coast from the spawning ground (Townsend et al., 1986; 1987). Seventeen egg bed sites were located between 1983 and 1987 based on information provided by local fishermen who observed herring eggs adhering to lobster pots which are deployed in large numbers along the coast to depths of 40-50 m (Figs. 2 & 3). Support from NOAA's National Undersea Research Program at the University of Connecticut, Avery Point, in 1985 and 1986 provided funding for surveys of individual spawning sites using a remotely-operated underwater vehicle (Mini-Rover) equipped with a video camera, depth gauge, and compass and deployed from a 40' support vessel.

The objectives of egg bed research activities in eastern Maine have been: 1) to precisely locate individual egg beds; 2) to determine the distribution and abundance of eggs at individual spawning sites in relation to depth, bottom topography, and substrate type, and; 3) to compare egg development and mortality rates at different positions in the egg mass, on different substrates, and at different distances from egg bed perimeters. Field work in the fall of 1985 produced video documentation of egg bed and spawning habitat characteristics at two sites (A & D). Two additional sites (F & K) were surveyed more extensively in the fall of 1986 and briefly in the spring of 1987. This paper presents a description of the physical characteristics of these four egg beds based on underwater video observations, bathymetric surveys, and observations and analyses of egg and sediment samples.

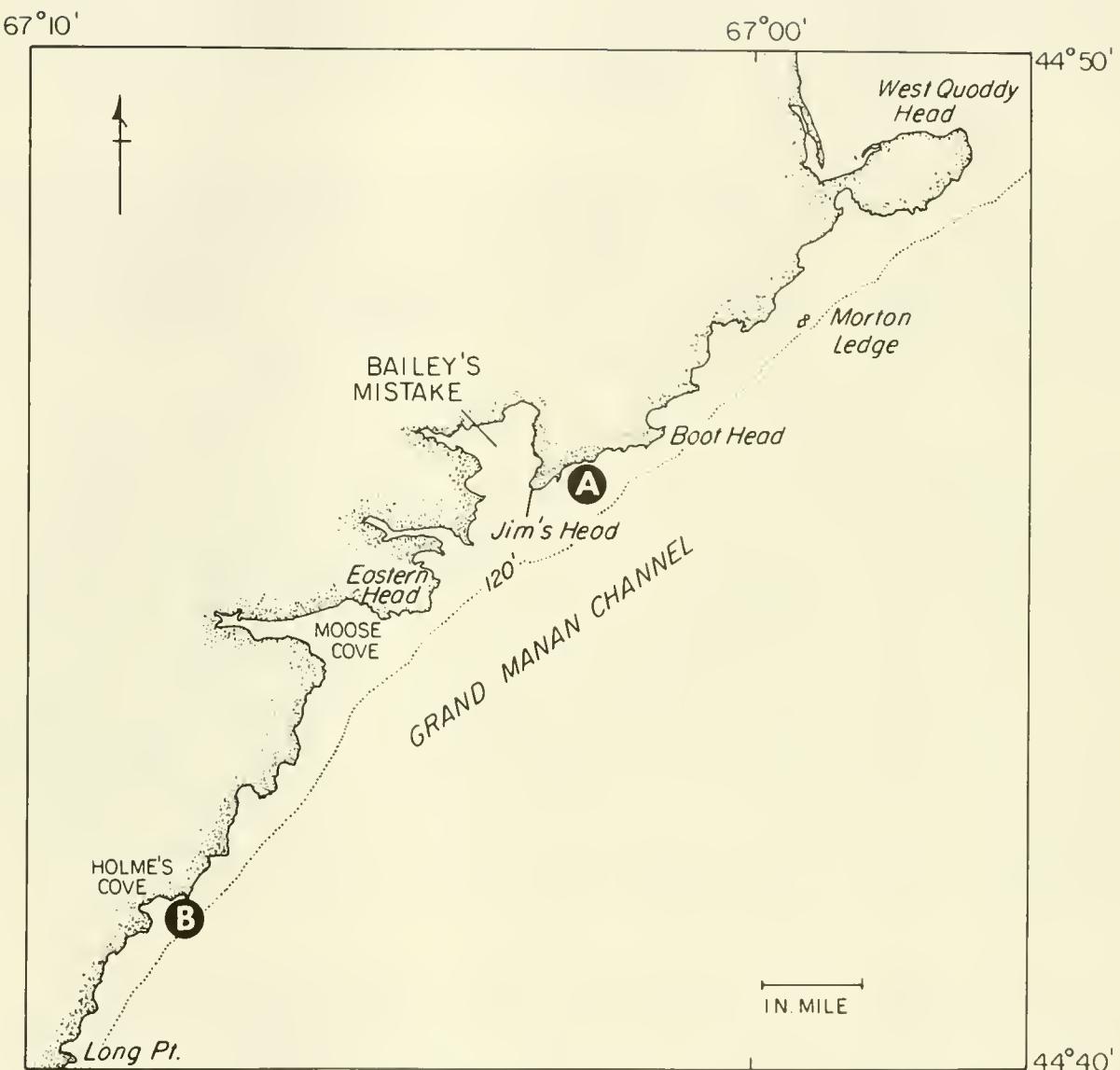


Figure 2: Individual herring spawning sites along the eastern Maine coast identified during 1983-87.

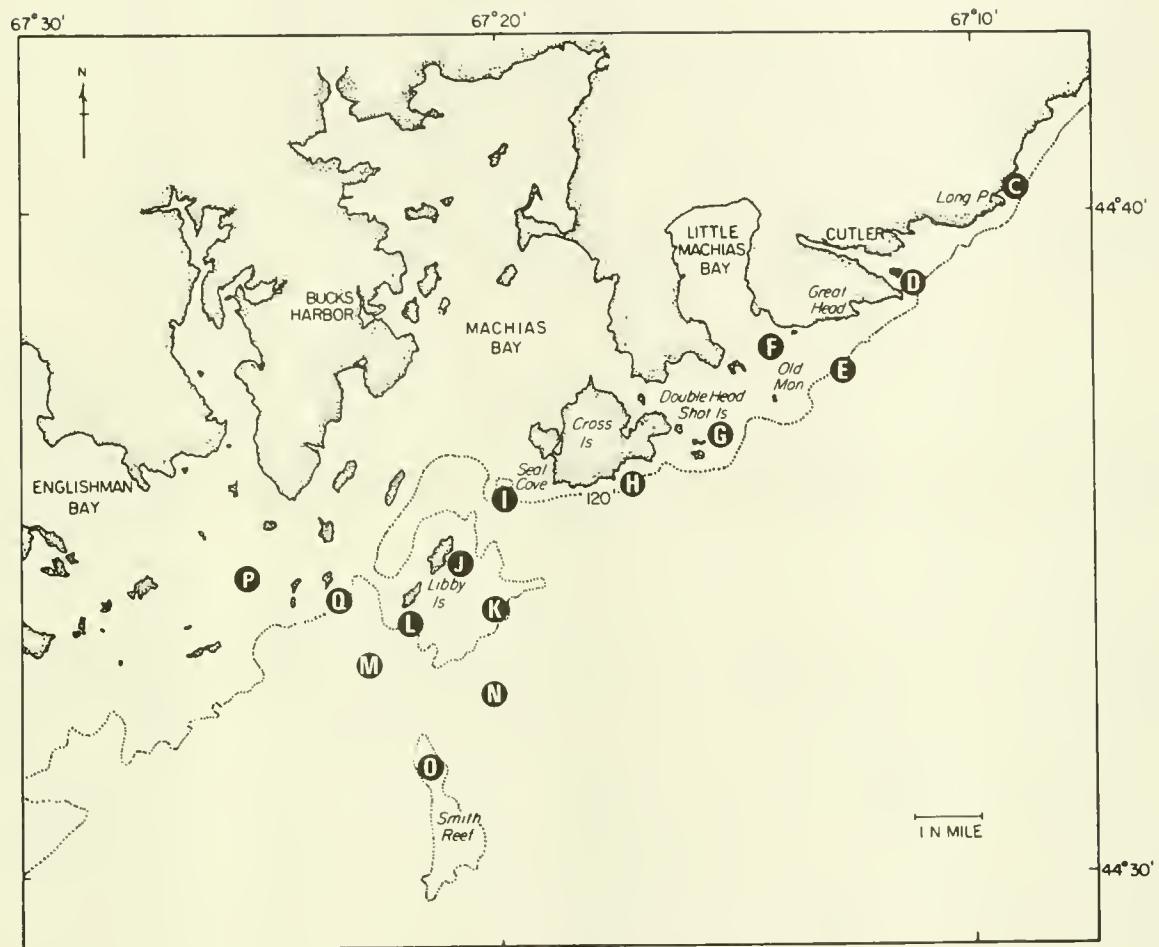


Figure 3: Additional herring spawning sites in eastern Maine identified during 1983-87.

METHODS

Field work was carried out during September 4-7 1985, September 8-October 3 1986, and July 7-8 1987. Field work in 1985 was limited primarily to video documentation with the Mini-Rover, but also included field observations of sediment samples collected inside and outside egg beds at sites A and D (Figs. 2 & 3). Field work in 1986 was more intensive and included, in addition to video observations, visual evaluation and analysis of egg and sediment samples collected with a Ponar bottom grab sampler deployed from the surface and, in depths of 25 m or less, by SCUBA divers. Detailed bathymetric surveys were conducted at sites F and K in 1986 with a depth recorder and, in July 1987, with a side-scan sonar. A few additional sediment samples were also collected with a Smith-MacIntyre benthic sampler at these same two sites in July 1987. Although these samples were not collected during the spawning season, information from the previous fall was used to differentiate samples from inside and outside the two spawning sites.

The ROV was used in both years for reconnaissance purposes and for surveying egg beds and spawning habitat. Reconnaissance dives were of short duration (10-15 minutes or less) and were used to confirm reports of egg deposition received from the fishermen, to precisely locate where eggs were deposited, and in 1986, to locate bottom areas that were suitable for sampling and to obtain video documentation of precise locations where samples were taken, both with the Ponar grab sampler and by SCUBA divers. In some cases, the ROV operator directed the grab sampling operation from the vessel by observing where the grab was in relation to the bottom and giving instructions for its final descent into the substrate. The ROV was also used to determine the extent of egg cover and to document changes in depth, bottom topography and general substrate type at different locations inside and outside of the egg beds. Special attention was paid to the perimeters of the egg beds in order to determine whether distinct changes in egg abundance could be related to changes in bottom topography and/or substrate. A total of 43 dives were made in 1986 in depths of 15-50 m, 12 at Libby Island and 25 at the Little Machias Bay (LMB) site (Fig. 4). Thirty-one dives were made in 1985 in depths ranging from 22 to 55 m at a variety of locations.

All dives were made from an anchored vessel using a 40 lb. down-weight and either a short (10 ft) or long (100 ft) tether to the ROV, depending on the state of the tide. Extreme tides in this part of the Gulf of Maine produce maximum current speeds along the coast of 2 knots at the surface and 1-1/2 knots at the bottom (Townsend et al., 1985). Transects as long as 1000 ft were successfully made in strong bottom currents by simply orienting the ROV downstream and maintaining visual contact with the bottom as anchor line was paid out. One to two hour dives with a long tether were made at slack water, using the down-weight as a central reference point. Visibility in eastern Maine

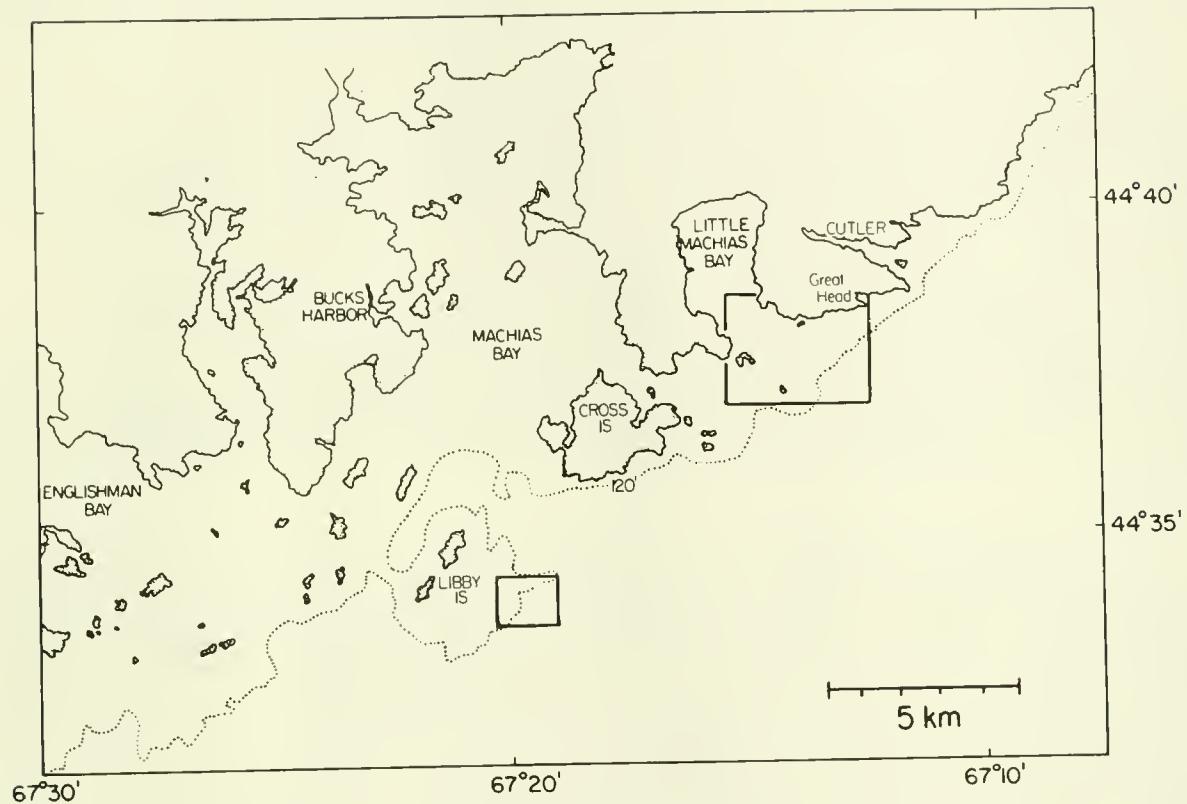


Figure 4: Spawning sites surveyed on the eastern Maine coast in 1986.

coastal waters is excellent since the strong tidal currents remove most of the fine sediments from the substrate.

Benthic samples obtained in the field were separated, when possible, into egg and substrate samples. Egg samples were preserved in a buffered 5-10% formalin solution; sediment samples were frozen. All samples were transported to the DMR Fisheries Research Laboratory in Boothbay Harbor for analysis. A total of 107 grab samples and about 20 SCUBA samples were collected in the fall of 1986. Of these, 72 of the grab samples and all the SCUBA samples were from the LMB site while 14 grab samples were collected at Libby Island. Egg and sediment samples collected in 1985 were not analyzed. Sediment samples collected in July 1987 were frozen and transported to Boothbay Harbor for analysis.

Egg mat samples collected in 1986 were subsampled (up to six subsamples per sample) with a small plastic core of known diameter. For mats of variable thickness, subsamples were taken at an equal number of thin and thick locations in the mat; for mats of more uniform thickness, subsamples were taken anywhere in the sample. Eggs in each subsample were counted and mean egg density and abundance (#/cc, #/m²) were estimated for each sample. The number of dead eggs in each subsample was also noted, as were any obvious differences in the stage of egg development. Most of the observations and samples collected in 1986 and 1987 were from Little Machias Bay (LMB); therefore, this egg bed was singled out for special attention in this paper.

RESULTS

Information obtained from local fishermen in 1985 resulted in the location of two spawning sites, a fairly large one east of Jim's Head (site A) and a smaller one near Western Head in the entrance to Cutler harbor (Site D). A continuous mat of eggs was first observed at Jim's Head in 30 m on September 9; these eggs were deposited on a flat bottom which was composed primarily of large shell fragments and gravel. The "edges" of this egg bed were distinct. At the eastern perimeter, the sediment type changed fairly abruptly to a much finer and more uniform sand and shell fragment substrate with large ripples, showing evidence of current action. No eggs were observed on rocks in shallower water nearer the shoreline. A few eggs were seen at Western Head on Sept. 12 in small, barely visible clumps and in small continuous patches in a similar depth and substrate as was observed at Jim's Head.

Two egg beds were located in eastern Maine coastal waters in 1986, one east of the Libby Islands and another near the entrance to Little Machias Bay (Fig. 4). As in the previous year, the initial information was obtained from fishermen. Herring apparently spawned at Libby Island on the night of Sept. 7-8 and at LMB on the night of Sept. 22-23. A large group of herring were repeatedly observed with depth recorders at the LMB site for about a week prior to spawning; samples of fish collected in a

gill net on the evening of Sept. 21-22 were fully mature. At both sites, eggs were first observed with the ROV within a day or two after spawning occurred.

The Libby Island site (Fig. 5) was in a more exposed location and in deeper water. Depths were fairly uniform, ranging from about 40 to 50 m (too deep for convenient SCUBA diving). Eggs were observed on lobster traps located 1.5 km apart in a NE-SW direction, but it is doubtful that the egg bed was continuous over these distances. Bad weather interrupted survey work for three days and most of the eggs had apparently hatched when operations resumed on Sept. 14. Egg bed observations and samples were therefore only obtained at this site during a two-day period (Sept. 9-10). Eggs were observed on the bottom in large clumps forming a more or less cohesive egg carpet at two locations. Where egg cover was heavy, the substrate was composed primarily of shell fragments. During one dive, an abrupt transition was observed between a rocky area with no eggs into a flat bottom with eggs. Egg cover increased as the distance from the rocks increased.

At the LMB egg bed site, surveying was continuous for a 10-day period from the morning after the fish spawned (Sept. 23) until the eggs started hatching (Oct. 2-3). The large number of bottom grab samples, SCUBA samples, Mini-Rover dives, and trap hauls made in this area provided fairly complete information concerning the distribution of eggs relative to depth and bottom features (Fig. 6). Eggs were deposited over an area approximately 0.8 km² in size. Negative grab samples delimited the inshore, offshore and western edges of the bed; the eastern edge of the bed was not as well defined. At 19 sampling locations distributed over most of the egg bed, a dense continuous carpet of eggs 1-3 cm thick was observed. At other locations, eggs, if present, were either moderate or few in number. Eggs were distributed at this site in two areas: 1) in a shallower (20-25 m) "pocket" between the shoreline and three rocky near-shore ledges; and 2) in deeper (25-35 m) water west and outside of these ledges and in between two near-shore islands. This is the area where the adult fish were congregating at right during the week prior to spawning.

Eggs were observed at this site on a variety of substrates including a thin veneer of eggs on small rocks near the inshore edges of the bed. Egg carpet was deposited on shell fragments and gravel. As at Libby Island, fairly abrupt transitions were observed between heavy egg cover in flat bottom areas to no eggs in adjacent rocky areas. The fish clearly avoided rocky, irregular, bottom areas when they spawned. Egg cover also diminished fairly abruptly in shallow water inside the entrance to Little Machias Bay (Fig. 6) on a more uniform, sandy substrate. The offshore edge of the egg bed was defined by increasing depth, but not an obvious change in bottom substrate. Egg density diminished more gradually through this perimeter of the egg bed until a point was reached where eggs did not form clumps and were

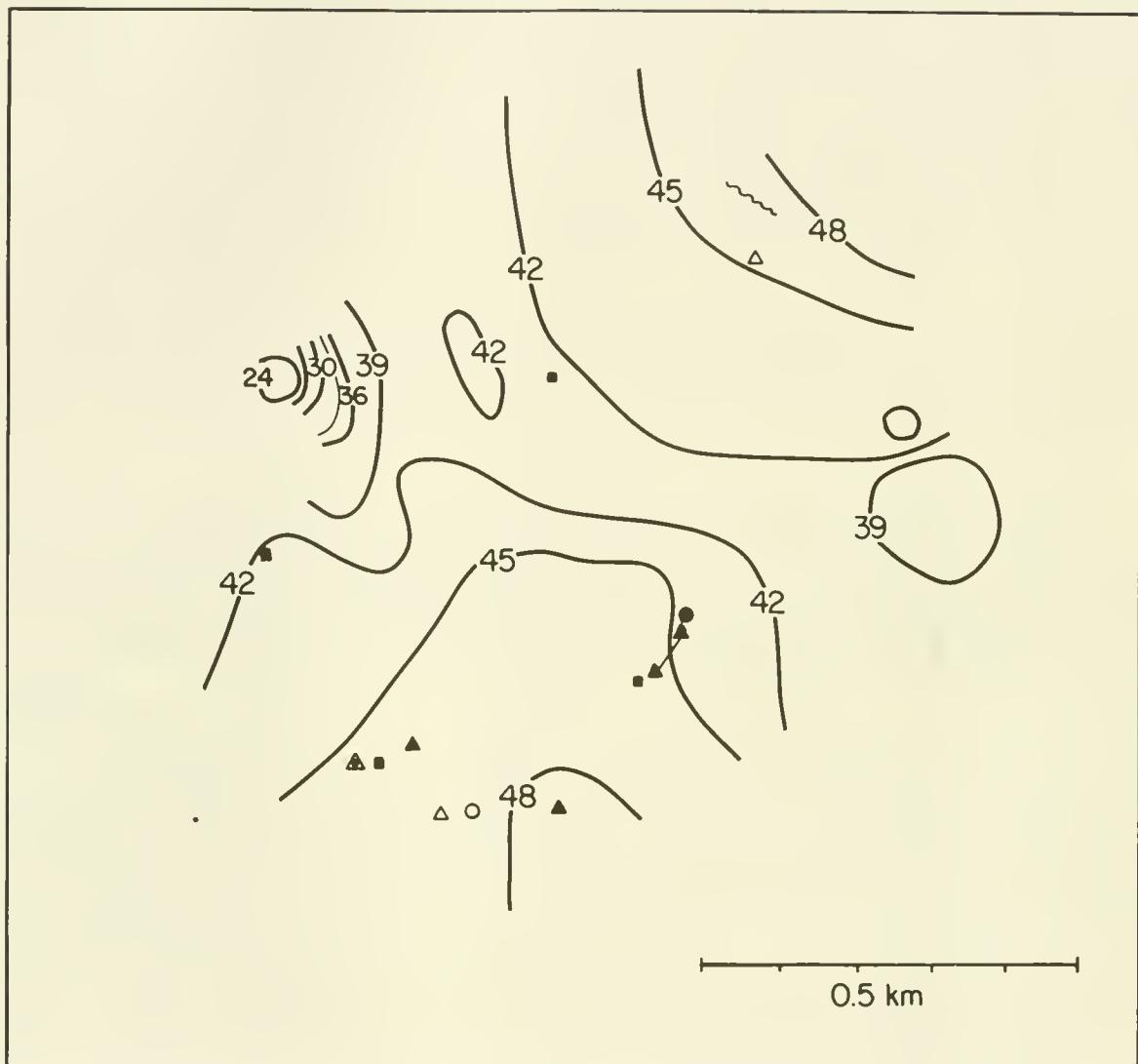


Figure 5: Small-scale map of the Libby Island egg bed site showing depth contours (m), and locations of ROV dives, bottom grab samples, and lobster traps where eggs were either present or absent (see Fig. 6 for legend).

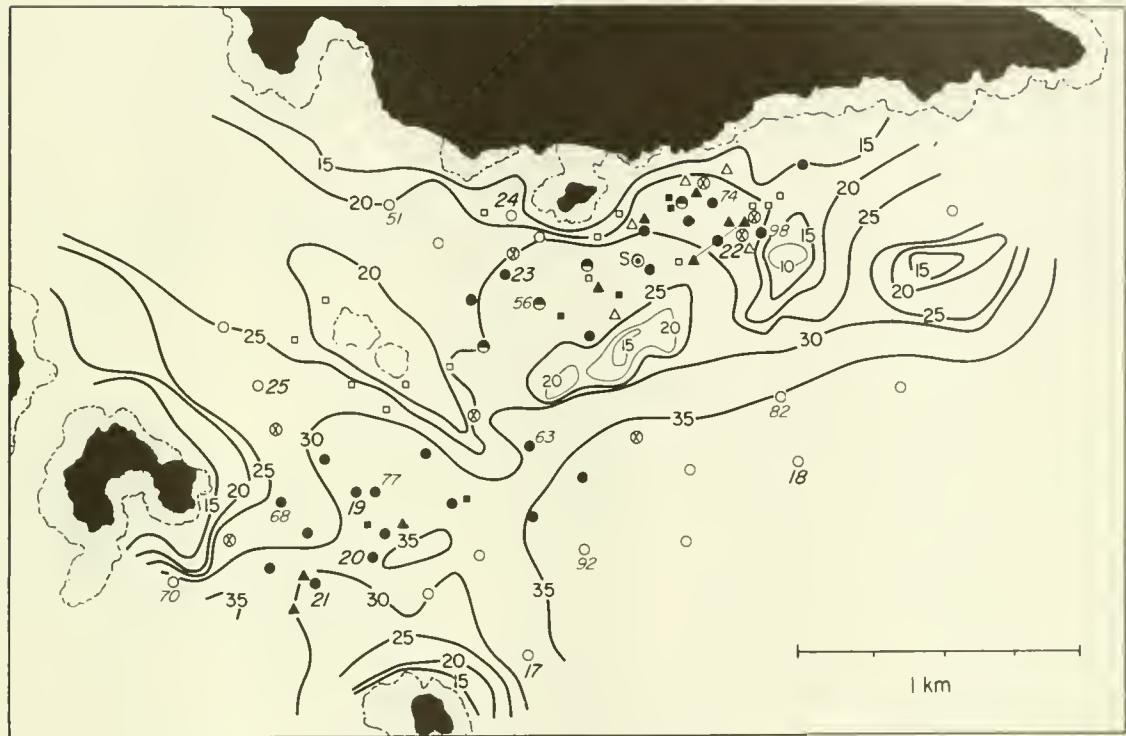


Figure 6: Small-scale map of the Little Machias Bay egg bed site showing the mainland, islands, nearshore ledges, depth contours (m), and locations of ROV dives, bottom grab samples, and lobster traps where eggs were either present or absent. Numbers in italics indicate positions where egg and sediment samples were collected (see Tables 1 & 2). Legend: \blacktriangle , \triangle = ROV dives with and without eggs; $\blacktriangle - \blacktriangle$ = ROV transect; \bigcirc , \otimes , \bullet , \blacksquare = grab samples without eggs, with very few eggs, a moderate number of eggs, and heavy egg cover; \blacksquare , \square = lobster traps with and without eggs.

mixed in with the sediments.

Analysis of 10 sediment samples collected at the LMB site with the Ponar grab sampler in 1986 (Table 1) failed to show any consistent difference in the percent composition by weight of shells, gravel, sand, and silt inside and outside the egg bed. Inside the egg bed (see Figs. 6 & 7), shells predominated at the two shallowest near-shore stations (98 & 74), gravel at two other stations (68 & 63), and sand at two stations (56 & 77). Silt and clay only reached appreciable amounts at the latter two locations. Outside the egg bed, gravel predominated in the entrance to the bay, sand at one of the deeper offshore stations, and shells at an offshore location and beyond the western extremity of the bed. Shells did not make up nearly as large a portion of the substrate at either of these two locations, however, as they did at stations 74 and 98, inside the egg bed.

Table 1: Percent composition by weight of shell, gravel, sand, and silt/clay in sediment samples collected with a Ponar grab sampler inside and outside the Little Machias Bay egg bed, September 1986.

<u>Inside Egg Bed</u>					
Sample	Depth (m)	%Shell	%Gravel	%Sand	%Silt/Clay
B98	20	87	4	8	1
B74	22	98	0	7	0
B56	25	18	28	37	17
B68	27	29	42	27	2
B63	32	32	41	27	0
B77	32	29	26	34	11

<u>Outside Egg Bed</u>					
	Depth (m)	%Shell	%Gravel	%Sand	%Silt/Clay
B51	20	11	55	28	6
B70	22	60	1	32	1
B82	32	52	10	34	4
B92	32	30	27	41	2

Analysis of 9 sediment samples collected with the Smith-MacIntyre sampler in July 1987 (Table 2) revealed clearer differences inside and outside of the same spawning site. Egg substrate in the inshore portion of the egg bed (stations 22 & 23) was composed primarily of shells or gravel; at the western end of the bed (stations 19-21), sand was the predominant sediment fraction. In none of the four samples collected outside the egg bed was there any noticeable quantity of gravel; the substrate was primarily shells at the two offshore stations (17 & 18) and sand at the two inshore stations (24 & 25).

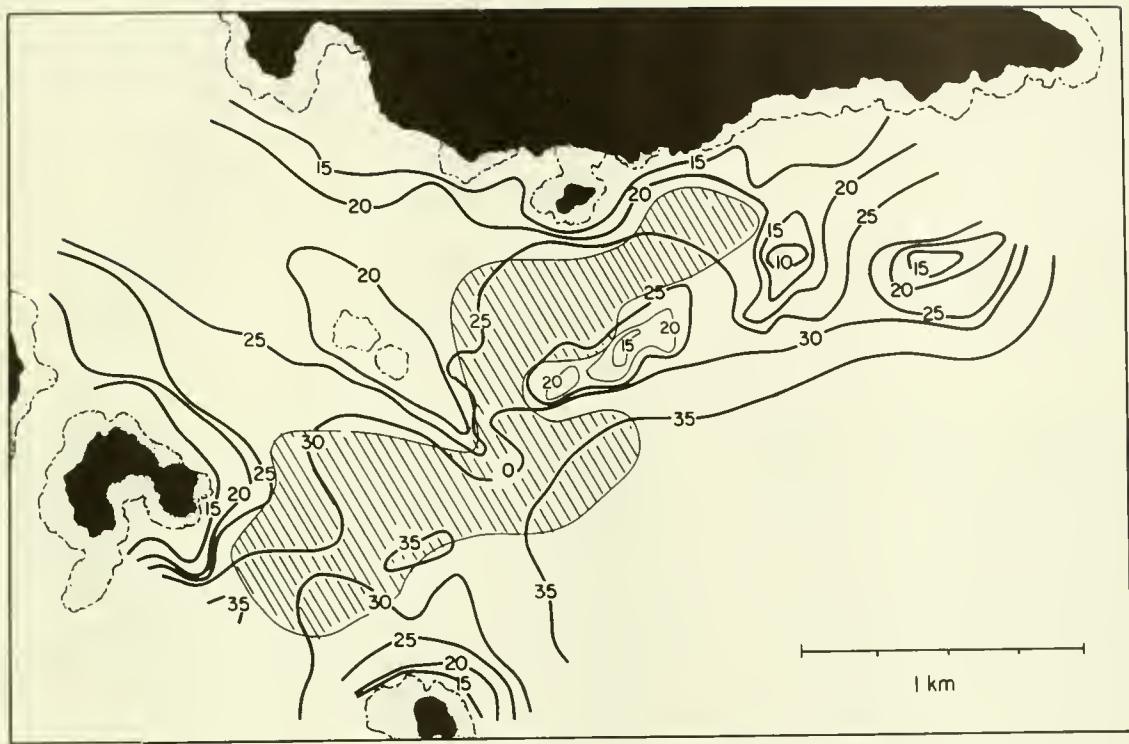


Figure 7: Approximate extent of egg deposition at the Little Machias Bay spawning site, September 1986.

Table 2: Percent composition by weight of shell, gravel, sand, and silt/clay in surficial sediments (top 1-2 cm) collected with a Smith-MacIntyre grab sampler inside and outside the Little Machias Bay egg bed, July 1987.

<u>Inside Egg Bed</u>					
Sample	Depth(m)	%Shell	%Gravel	%Sand	%Silt/Clay
SM-19	32	35	16	45	4
SM-20	32	32	25	42	2
SM-21	30	21	27	47	4
SM-22	24	77	3	20	1
SM-23	24	34	48	19	0
<u>Outside Egg Bed</u>					
SM-17	23	80	1	13	6
SM-18	35	57	2	39	2
SM-24	22	15	0	83	2
SM-25	24	12	0	80	8

These results suggest that gravel is an important component of egg substrate, although egg substrate is clearly a mixture of shell fragments, gravel, and sand and can be almost 100% shells. This conclusion could not be reached from analysis of the Ponar samples because of a difference in gear design and performance. The Ponar grab collects a much more disturbed substrate sample than the Smith-MacIntyre grab; only in the Smith-MacIntyre samples was it possible to collect the top 1-2 cm of sediment. Surficial sediments in fact compose the egg substrate, i.e., that portion of the substrate to which the eggs are attached. Additional surficial sediment samples are required to test the hypothesis that herring do not deposit eggs on substrates with little or no gravel. Drapeau (1973) reported that herring spawned on Georges Bank in 1970 exclusively on gravel patches devoid of sand.

Analyses of three samples of egg carpet obtained with the Ponar grab sampler and seven collected by SCUBA divers revealed significant differences in egg density and abundance between the shallow and deep portions of the LMB egg bed (Table 3). Mean egg density was 35% higher in the deeper water and mean egg abundance was almost twice as high. These results indicate that the egg mat was denser and thicker in deeper water. The range of egg abundance estimates for all 51 sub-samples was 1.2-7.2 million eggs/m² with means of 2.5 million in the shallower portion of the bed and 4.4 million in deeper water. Multiplication of these two mean egg abundance estimates times the areas of the two portions of the egg bed produced a rough estimate of 3.1×10^{12} eggs in the entire egg bed (Table 4). A more conservative estimate based

on a 50% reduction in mean egg abundance estimates was 1.6×10^{12} eggs. High and low estimates of the biomass of spawning fish that spawned at this location were 14,900 and 7,800 metric tons, based on the mean length and weight of 44 fish caught in a gill net 24 hours before spawning occurred and published estimates (Kelly and Stevenson, 1985) of fecundity for the coastal Maine stock for 1982. This was apparently a large school of fish since annual estimates of age 4+ spawning stock for the entire Gulf of Maine stock between 1975 and 1982 only ranged from 50,000 to 100,000 tons (Fogarty and Clark, 1983).

Table 3: Herring egg density and abundance in shallow and deep water, Little Machias Bay, as estimated from intact egg mat fragments collected with a Ponar grab sampler (B samples) and by SCUBA divers (S samples), September 1986.

Shallow Water (22-25 m)

Sample	Thickness (mm)	N	Density (#/cc)		Abundance (#/ $m^2 \times 10^6$)	
			Mean	Range	Mean	Range
B62	8-25	3	248	154-296	3.2	2.9-3.6
B74	10-20	6	159	94-212	2.2	1.7-2.9
B95	10	4	213	180-242	2.1	1.8-2.4
S7	15	3	225	182-263	2.2	1.8-2.6
S8	20	1	269	---	2.7	---
S10	10-20	3	192	125-251	2.3	2.0-2.5
S12	10-15	3	200	124-242	2.5	1.2-3.6
S13	12-17	3	216	202-232	2.9	2.6-3.4
S14	8	1	282	---	2.3	---
S15	10	3	312	277-332	3.1	2.8-3.0
	8-25	30	217±23	94-332	2.5±.22	1.2-3.6

Deep Water (31-34 m)

Sample	Thickness (mm)	N	Density (#/cc)		Abundance (#/ $m^2 \times 10^6$)	
			Mean	Range	Mean	Range
B63	7.5-30	6	338	299-454	4.9	3.2-7.2
B65	10-15	3	252	251-253	3.0	2.5-3.8
B68	7-11	3	321	298-341	2.9	2.1-3.8
B77	10-26	6	263	185-314	4.5	2.6-7.0
B79	20-27	3	265	224-312	6.3	6.0-6.7
	7-30	21	292±24	185-454	4.4±0.7	2.6-7.2

Table 4: Estimated biomass of herring which spawned at the Little Machias Bay egg bed in September, 1986.

	<u>High Estimate</u>	<u>Low Estimate</u>
<u>Shallow Water:</u>		
Area of egg bed	$0.3 \times 10^6 \text{ m}^2$	$0.3 \times 10^6 \text{ m}^2$
Mean egg abundance	$2.5 \times 10^6/\text{m}^2$	$1.2 \times 10^6/\text{m}^2$
Total # eggs	0.8×10^{12}	0.4×10^{12}
<u>Deep Water:</u>		
Area of egg bed	$0.5 \times 10^6 \text{ m}^2$	$0.5 \times 10^6 \text{ m}^2$
Mean egg abundance	$4.4 \times 10^{12}/\text{m}^2$	$2.2 \times 10^{12}/\text{m}^2$
Total # eggs	2.3×10^{12}	1.2×10^{12}
<u>Entire Egg Bed:</u>		
Total # eggs	3.1×10^{12}	1.6×10^{12}
Mean length of fish	29.6 cm TL	29.6 cm TL
Mean weight of fish	0.24 kg	0.24 kg
Fecundity (29.6 cm TL)	1×10^5 eggs	1×10^5 eggs
# spawning females	3.1×10^7	1.6×10^7
# spawning fish (1:1 sex ratio)	6.2×10^7	3.2×10^7
Biomass of spawning fish (0.24 kg/fish)	14.9×10^3 MT	7.8×10^3 MT

Egg mortality rates were negligible. Percentages of dead eggs estimated from the same sub-samples were all <5%; most of them were 1% or less. Low egg mortality rates prevailed through September in a sample collected the day that the eggs began to hatch. No evidence of egg predation was observed, although cod are known to sometimes congregate in the vicinity of egg beds on this spawning ground and feed actively on herring eggs. In all samples collected prior to October 2, no obvious differences in the stage of egg development were discerned, indicating that all eggs were probably spawned at more or less the same time. In one sample collected on October 2, eggs could be divided into two distinct groups, i.e., eggs with and without black eye pigmentation. Eggs in more and less advanced stages of development in this sample were clustered in distinct groups, but there was no clear relation between the stage of development and position in the egg mass. These preliminary results suggest that, not only is egg mortality low in egg mats 1-3 cm thick deposited along the

eastern Maine coast, but eggs deposited on the underside of the egg mat develop at the same rate as those at the top. Two implications of these preliminary observations are that eggs spawned during a single night probably hatch during a very short period of time and that most mortality occurs at hatching and/or in the larval stage.

DISCUSSION

Spawning at the Little Machias Bay site in September, 1986 produced a relatively large egg bed with several characteristics which distinguished it from other fall-spawned egg beds in the Gulf of Maine reported on by other authors. First of all, the egg mat was fairly thick, measuring from 1-3 cm or up to 20-30 eggs deep; as a result, egg density and abundance were also high. At other deep-water sites in the Gulf of Maine, egg mats 1-2 cm and 4-5 cm thick have been reported on Georges Bank and Jeffreys Ledge (Caddy and Iles, 1973; McCarthy et al., 1979). However, at most of the spawning sites surveyed in the Jeffreys Ledge area, egg cover was considerably thinner; sometimes the egg layer was only a single egg thick. Messieh et al. (1987) reported maximum thickness of over 5 cm for portions of an egg bed 1.1 km² in size located in 15-20 m on Fisherman's Bank, Prince Edward Island (Gulf of St. Lawrence) surveyed in September, 1986. Five smaller spawning sites were located in the same area in 1985 in depths of 10-25 m; egg deposition reached thicknesses of 20-30 eggs or 4.5 cm (Messieh & Rosenthal, 1986). Mean egg abundance estimates were extremely variable, ranging from 4.7×10^3 to $7.9 \times 10^6/m^2$ at the five sites. Maximum abundance estimates at LMB in 1986 reached $6.3 \times 10^6/m^2$ at one station and averaged $4.4 \times 10^6/m^2$ in depths of 31-34 m. McKenzie (1964) reported that Atlantic herring egg carpets in shallow water (11-13 m) off southwest Nova Scotia reached 3.25 cm. Egg density estimates at the LMB site reached maximum values in excess of 400 eggs/cc. Bowers (1969) reported values of only 30-165 eggs/cc in egg layers up to 9 layers deep at deep-water spawning sites near the Isle of Man in the English Channel.

Secondly, despite a fairly dense concentration of eggs at the LMB site, egg mortality was extremely low and there was no evidence of significantly different egg development rates at any position in the egg mass. In contrast, Cooper (personal communication) reported that 50-70% of the eggs in the lower portion of an egg mat 4-5 cm deep near Jeffreys Ledge were non-viable. Other authors have reported high egg mortalities and low hatching success in egg masses reaching 16-20 layers or 5×10^6 eggs/m² (Galinka, 1971) as well as a reduced hatching rate (Hourston et al., 1984; Taylor, 1971). However, these studies were conducted with Pacific herring spawning in very shallow water. However, egg bed surveys conducted recently in the Gulf of St. Lawrence in 10-25 m (see above) also reached extremely high egg mortalities and retarded and abnormal embryonic development. In 1986, mortality rates reached 95% in egg mats which averaged only 2 cm thick due to poor circulation and lack of oxygen. "Mass

"mortalities" were reported the previous year in a "solidly packed" mat up to 30 egg layers deep (4.5 cm); abnormal embryonic development was reported at all levels below the top egg layer. In contrast, Cooper et al. (1975) estimated that hatching success exceeded 99% at one of their dive sites near Jeffreys Ledge where egg cover was sparse. No estimates of hatching success were made in eastern Maine, but the complete absence of any decaying egg residues following hatching at Jim's Head in 1985 suggests that hatching success on egg beds in eastern Maine is high. The eastern Maine coast appears to provide optimum conditions for herring egg deposition and survival. Two major reasons for this are probably the strong bottom tidal currents which provide plenty of aeration to support egg metabolism and development and coarse bottom sediments (which are a consequence of strong currents) which provide a stable egg substrate.

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